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Natural products from Western Australian marine organisms

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Abstract

The natural products isolated from marine organisms found in Western Australia are reviewed. Although over 110 different compounds have been identified these result from only a preliminary survey of sponges, a few examples of other marine fauna, algae and sea grasses. The discussion takes a chemotaxonomic approach highlighting the sources of the metabolites and the uniqueness or otherwise of the metabolites occuring in organisms available in Western Australia. The biological activity of some of these metabolites is noted. In the Appendix the structures of all compounds identified are presented together with the source organism and, where the information is available, the proportion of each metabolite of the dry weight of the organism. The information contained in this review should serve as a starting point and a stimulus for more detailed studies of the biology, chemistry and ecology of the Western Australian marine environment.

Introduction

Marine natural products chemistry has experienced a rapid growth in recent years. Organic chemists have recognized that the seas and oceans, which contain an estimated 500 000 species of plants, animals and microbes, are a major source of new natural products and their study is being vigorously pursued. In Australia research in marine natural products received little consideration before 1960. (For a summary of the early interest by biologists in Australian marine natural products research see Baker 1976).

Studies into the chemistry of Australian marine organisms began in Queensland in the late 1950s with Sutherland, who was mainly involved in the isolation and identification of quinonoid pigments from the crinoids of the Great Barrier Reef. The accessibility of diverse marine life of the Great Barrier Reef to a number of Australian research institutions together with the advent of more efficient collection procedures (*ie* SCUBA) made research into marine natural products feasible in those centres. The Roche Research Institute of Marine Pharmacology (RRIMP) during its period of operation (April 1974 - June 1981) undertook a systematic examination of numerous marine organisms from the eastern Australian coast in a search for commercially viable biologically active compounds (Wells 1979). However little information is available from this source on the marine natural products from the coastal waters of Western Australia. This coastline, bounded to the south by the cold waters of the Southern Ocean, extends to subtropical and tropical waters in the north. The coastal topography includes extensive limestone cliffs, rocky and sandy beaches, coral reefs and mangrove communities. Many of these differing environments may harbour new and indigenous species of flora and fauna, some perhaps possessing novel chemistry.

In embarking on an investigation of the natural products from marine organisms of the Western Australian coast we chose to limit ourselves to the Porifera and Marine Algae, which have proved prolific sources of natural products elsewhere. During the preliminary period of this investigation collections were restricted to shore based 'dives' (SCUBA and snorkel) and 'beachwash', along the coast from Augusta to Lancelin, together with several trips to reefs off Perth. With the availability of the marine research vessel 'Uniwest' to the University of Western Australia the potential for more ambitious collections was realized. An expedition to the Abrolhos Islands in May 1981 provided many interesting specimens as well as a valuable test for 'onboard' procedures.

This paper presents a review of the natural products chemistry of Western Australian marine organisms collected by us and includes work carried out by other groups which have published work on the topic. We hope that this review, which essentially is an inventory of organic chemicals available in Western Australian waters, will provide a starting point and stimulus for further study of the biology and chemistry of Western Australian marine environments. Note that in the text numbers in bold face refer to compounds whose structural formulae are presented in numerical order in the Appendix.

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Porifera

Marine fauna of the phylum Porifera, sponges, are difficult to classify taxonomically as many of their morphological features differ with environmental as well as genetic variations. Even chemotaxonomic observations require careful interpretation since sponges can exist in symbiosis with blue-green algae and bacteria, yielding natural products with uncertain biogenetic origins (Berquist & Wells 1983). Table 1 is a list of sponges collected in Western Australia which have been investigated for secondary metabolites.

Sponges are classified into one of four classes, Calcarea, Hexactinellida, Sclerospongiae or Demospongiae, based on the chemical and structural nature of their skeletal material (Bergquist 1978). The Demospongiae constitutes the most diverse and ecologically significant group and information on this class has dominated the literature on sponge natural products. The majority of Australian Demospongiae examined for interesting secondary metabolites are members of the order Dictyoceratida, in which the inorganic sponge skeleton of the other orders is replaced by an organic fibrous network. Sponges of this order can be grouped into three families, Dysideidae, Spongiidae and Thorectidae (Bergquist 1978). The Dysideidae is a small family containing only one large genus, *Dysidea*. Two members of this family, *Dysidea* and an undetermined genus, have been collected off the West Australian coast and examined chemically (Capon 1982, Dunlop, Ghisalberti & Jefferies, unpublished results). Both were found to produce examples of furanosesquiterpenes, (**1-4**) and (**1,2**) respectively, previously isolated from *Dysidea* species, *eg D. herbacea*, from the Great Barrier Reef. *Dysidea* species provide a number of different sesquiterpenoid skeletons and have proved consistent in producing this type of terpenoid metabolite. The presence in some *Dysidea* of non-terpenoid halogenated metabolites has been ascribed to involvement of extraneous microorganisms, particularly cyanophytes (Bergquist & Wells 1983).

From the Spongiidae family samples of several genera, *Phyllospongia, Spongia, Leiosella, Lendenfeldia* and an undetermined genus have been studied. Specimens of a *Phyllospongia* sp collected off Burns Beach and of an undetermined genus of the Spongiidae did not yield any recognisable metabolites. In common with other Australian *Spongia* species the specimen from Western Australia contained a C_{21} difuranoterpene (**5**) (Capon *et al* 1982a) Although **5** is a new compound it is related to other dominant *Spongia* metabolites. The *Leiosella* sp investigated also contained similar terpenes (**6,7**) (Capon *et al* 1982a) previously isolated from *Spongia* species from New South Wales and Victoria. In addition to the two C_{21} furanoterpenes (**8,9**) a *Lendenfeldia* sp also produces a set of cyclic sesterterpenes (**10-14**) (Kazlauskas *et al* 1982b). This places *Lendenfeldia* taxonomically closer to *Carteriospongia* and makes these two genera distinct from *Spongia*. *Spongia* represents a point of close similarity to genera within the Thorectidae, which with 14 genera is the largest family of the Dictyoceratida and morphologically the most diverse.

Several collections of *Ircinia* from Shark Bay were shown to contain the linear sesterterpene tetronic acids (**15,16**) and minor amounts of a mixture of sterol epidioxides (**17-19**) (Cassidy 1982). On the other hand an *Ircinia* sp from Rottnest yielded squalene (**20**), furospinosulin (**21**), the logical precursor of the tetronic acid (**15**), as well as the

Table 1

Western Australian Sponges (Class: Demospongiae) mentioned in this review

Sub-Class	Order	Family	Genus	Collection site	Specimen number
Ceractinomorpha	Dictyoceratida	Dysideidae	undet. genus*	Gun Island, Houtman Abrolhos	WAM 430-81
			Dysidea	Lefebre Island	SB 036
		Spongiidae	*Lendenfeldia*	Quobba Lagoon	
			Spongia	Gun Island, Houtman Albrolhos	WAM 429-81
			Leiosella	Rottnest Island	WAM 83-82
			undet. genus	Lancelin	WAM 147-82
			Phyllospongia	Burns Beach	WAM 403-80
		Thorectidae	*Ircinia*	Wooramel Delta	WAM 44-82
					WAM 148-82
					WAM 149-82
				Mewstone, Rottnest	WAM 16-82
			Thorectandra	Carnac Island	WAM 84-82
	Poecilosclerida	Clathriidae	*Clathria*	Carnac Island	WAM 51-82
		Desmacidonidae	*Desmacidon*	Carnac Island	WAM 53-82
	Haplosclerida	Haliclonidae	*Haliclona*	Cosy Corner, Hamelin Bay	WAM 425-81
		Adociidae	*Adocia*	Carnac Island	WAM 17-82
		Callyspongiidae	new genus	Cosy Corner, Hamelin Bay	WAM 17-82
			undet. genus	Rottnest Island	WAM 431-81
			Dactylia	Carnac Island	WAM 47-82
				Rottnest Island	WAM 14-82
	Halichondrida	Halichondriidae	*Halichondria*	40 km west Lancelin	WAM 14-82
	Verongida	Verongidae	*Iotrochota*	Five Fathom Bank, Fremantle	
Tetractinomorpha	Choristida	Jaspidae	*Jaspis*	Carnac Island	WAM 54-82
	Hadromerida	Suberitidae	*Suberites*	Carnac Island	WAM 52-82
		Spirastrellidae	*Spirastrella*	Carnac Island	WAM 49-82
	Axinellida	Desmoxyiidae	*Higginsia*	40 km west Lancelin	WAM 145-82
	Dendroceratida	Aplysillidae	*Chelonaplysilla*	Carnac Island	WAM 48-82

* Classification is doubtful
† Specimens with WAM prefix have been lodged with the Western Australian Museum

analogues (**22**) and (**23**) (Capon 1982). A *Thorectandra* sp yielded **21** and the indole salt (**24**) derivative of aplysinopsin (Capon 1982) previously isolated from other Australian *Thorectandra* species and *Fascaplysinopsis reticulata*, which has many features in common with *Thorectandra*.

Two samples of the order Poecilosclerida, *Clathria* (Family: Clathriidae) and *Desmacidon* (Family: Desmacidonidae) have been collected. Preliminary analysis failed to reveal distinct metabolites.

A *Haliclona* sp (Order: Haplosclerida; Family: Haliclonidae) collected at Hamelin Bay contained two new cyclic ethers (**25,26**) (Capon *et al* 1982b). The Callyspongiidae are in the same order and were represented in our collection by three genera, *Dactylia* sp, a new genus and an undetermined genus. From the *Dactylia* sp only 4-hydroxybenzaldehyde (**27**) could be identified (Capon 1982). The metabolites of the other two collections were similar (**28-30**) and belong to an unusual group of polyhalogenated biphenyl ethers (Capon 1982, Capon *et al* 1981c). This group of metabolites have also been found in *Dysidea herbacea*. *D. chlorea* and *Carteriospongia foliascens*. These results when taken together are of interest particularly if one notes that many *Casteriospongia* species are known to contain high levels of blue-green algae within their matrix. It seems that these metabolites could arise from the algae or from a combination of algal-sponge metabolism.

Three new sesquiterpenes (**31-33**) and (-)-β-bisabolene (**34**) were isolated from the only specimen of the order Halichondrida, *Halichondria* sp, collected (Capon *et al* 1982c). The sesquiterpenes accounted for 11.2% of the dry biomass. A brominated indole derivative (**35**) was the major metabolite isolated from *Iotrochota* sp, a member of the Verongida family (Dellar *et al* 1981). Specimens of *Jaspis*, *Suberites* and *Spirastrella* were also collected and analysed but did not yield distinct metabolites. The last sponge to be considered is a *Higginsia* sp (family: Desmoxyiidae). Since its classification in 1945 there appear to have been only a small number of collections of this genus including the detection of spicules of *Higginsia* sp in the gut of nudibranchs (Thompson *et al* 1982). The WA specimen yielded a mixture of four novel diterpenes (**36-39**) (Cassidy *et al* 1985).

Other marine fauna

For the sake of completeness mention should be made of isolated studies on other WA marine fauna. From a compound ascidian collected in the Abrolhos, the blue pigment (**40**) was isolated (Kazlauskas *et al* 1982a).

Echinodermata are abundant in Western Australian waters and they are collected adventitiously in large numbers in the nets of prawn trawlers operating in Shark Bay. Many species are brilliantly coloured and their ready availability made them suitable organisms for a marine natural products study.

There are five classes of echinoderms: Asteroidea (starfish), Ophiuroidea (brittle star), Echinoidea (sea urchin), Holothuroidea (sea cucumber) and Crinoidea (feather star). All five classes contain carotenoids which may be either "carotenes" or "xanthophylls". In the asteroids, alcoholic xanthophylls are often bound to integumentary proteins, differences between which probably account for the wide variations in colours often observed among different specimens of the same species (Grossert 1972). Sixteen species of echinoderms (Table 2) collected from Western Australian waters were examined for the presence of pigments and terpenoids. Terpenes were not detected. Eleven of these, within the class Holothuroidea (one), Ophiuroidea (six), Echinoidea (three) and Asteroidea (one) contained either no extractable pigment or very little. Three of the five remaining species (Crinoidea) were rich in pigments. *Comantheria briareus* yielded the linear naphthopyrones (**41-43**) and the angular naphthopyrone (**44**). *Comathula solaris* afforded the anthraquinones (**45,46**) and *C. rotolaria* yielded (**46,47**) (Francesconi 1980, 1983).

Table 2

List of Echinoderms investigated for presence of pigments and terpenes

Class	Family	Species
Holothuroidea	Cucumariidae	*Pentacta crassa* (Ekman)
Ophiuroidea	Euryalidae	*Euryale aspera* (Lamarck)
	Gorgonocephalidae	*Astroboa granulatus* (H L Clark)
		Astroboa nuda (Lyman)
	Ophiotrichidae	*Ophiothrix ciliaris* (Lamarck)
		Ophiothrix (Acanthophiothrix) aff. *purpurea* (von Martens)
		Ophiomaza cacaotica (Lyman)
Echinoidea	Temnopleuridae	*Holopneustes porosissimus*
		Salmacis virgulata
	Citaridae	*Prionocidaris bispinosa* (Lamarck)
Crinoidea	Comasteridae	*Comatula rotalaria* (Lamarck)
		Comatula solaris (Lamarck)
		Comantheria briareus (Bell)
		Comanthina belli (P H Carpenter)
	Himerometridae	*Amphimetra tessellata* (J Muller)
Asteroidea	Metrodiridae	*Metrodira subulata* (Gray)

Arsenobetaine (**48**) has been isolated from the tail muscle of the western rock lobster (*Panulirus cygnus*) (Cannon *et al* 1981), from the flesh of the dusky shark (*Carcharinus obscurus*) (Cannon *et al* 1981), both of which are commercially important seafoods, and in the flesh of the school whiting (*Sillago bassensis*) (Edmonds & Francesconi 1981a). The arsenic containing ribofuranosides (**49,50**) have been isolated from the kidney of the giant clam, *Tridacna maxima* taken from Shark Bay (Edmonds & Francesconi 1982). It has been suggested that these compounds are metabolic waste products of the zooxanthellae present in clam tissue and that their biosynthesis is a general response of algae to oceanic arsenate.

Algae

The marine algae consist of those structurally simple marine plants without roots, stems or leaves and having primitive methods of reproduction. Commonly known as seaweeds they may be of macroscopic or microscopic form and collectively are the basis of all marine food chains. Macroalgae, the subject of our investigations, fall into three divisions: Chlorophyta (green), Phaeophyta (brown) and Rhodophyta (red). The Cyanophyta (blue-green) which are procaryotic, constitute a less accessible, but none the less important, fourth division (Price 1981).

Unlike the Porifera it is possible to classify taxonomically many algae to at least the genus level 'in the field' based on their macroscopic characteristics. Although 'colour coded' into divisions, colour is sometimes not a reliable guide, Rhodophyta growing in intertidal zones often appear brownish or even yellow rather than red. Classification to the species level sometimes requires detailed microscopic examinations. Table 3 lists Western Australian algae which have been studied as sources of natural products.

The Chlorophyta are distinguished from other algae by the presence of chlorophyll b in the pigment complex, the synthesis and storage of starch as the predominant reserve material and motile cells (McRaild 1981). Of the little published data on the natural products from Australian Chlorophyta most is concerned with the genus *Caulerpa*, which is widely distributed in tropical and temperate Australian waters. Several species of *Caulerpa* were collected from Western Australian waters and examined for metabolites and two distinct groups were identified. *C. flexilis* var *muelleri* and *C. trifaria* produced the sesquiterpenes (**51,52**) and the diterpene (**53**) respectively (Capon *et al* 1981a, Capon *et al* 1983). These compounds were new but are biogenetically related to compounds previously isolated from *C. brownii*, *C.flexilis* and *C. trifaria* from the eastern seaboard (Wells 1979). Samples of *C. brownii*, *C. flexilis*, *C. peltata* and *C. racemosa* collected at different points along the WA coast did not yield terpenoid metabolites and the last two contained the pigment caulerpin (**54**) (Capon *et al* 1983). Such observations are not uncommon in marine natural products chemistry and can be explained by considering variations in environment *ie* stress or geographical variants with differing secondary metabolism but similar morphological structure.

Unlike the Chlorophyta which can be found in both marine and freshwater environments the Phaeophyta are almost entirely marine (Clayton 1981). Ranging in size from thin crusts to massive kelps the brown algae are the most conspicuous seaweeds of rocky temperature shores making them an obvious source of material for the marine natural products chemist. Of more than 100 genera of brown algae recorded from the shores and subtidal regions of Australia and New Zealand about one quarter are endemic (Clayton 1981).

Two samples of the order Fucales, family Cystoseiraceae, have been examined. An unclassified *Cystophora* sp yielded the carotenoids, β-carotene (**55**) and fucoxanthin (**56**), the phytosterol fucosterol (**57**) and three new derivatives (**58-60**) of geranyl toluquinol (Capon *et al* 1981b). *Caulocystis uvifera* produces the antiinflammatory salicylic acid (**61**) the linear alkene (**62**) and ketones (**63-65**), and qualitatively is similar to *C. cephalornithos* (Capon 1982). A *Sargassum* sp (family: Sargassaceae) contained the prenylated derivatives of toluquinol (**66,67**) (Arrowsmith 1983).

Table 3

Western Australian Algae examined for secondary metabolites*

Division	Class	Order	Family	Genus	Collection site
Chlorophyta	Chlorophyceae	Caulerpales	Caulerpaceae	*Caulerpa brownii* Endlicher	Augusta to Lancelin
				Caulerpa flexilis (Lamx.) var. *muelleri* (Sond.)Wom.	Cosy Corner
				Caulerpa peltata Lamouroux	Big Nook, Houtman Abrolhos
				Caulerpa racemosa (Forssk.)J.Ag.	Augusta to Lancelin
				Caulerpa trifaria Harvey	Point Peron
Phaeophyta	Phaeophyceae	Fucales	Cystoseriraceae	*Cystophora* sp	Hamelin Bay
				Caulocystis uvifera (C.Ag.)J.Ag.	Wreck Point
			Sargassaceae	*Sargassum* sp	Big Rat Island Lagoon
		Dictyotales	Dictyotaceae	*Dictyota furcellata* (C.Ag.)J.Ag.	Cape Peron, Shark Bay
				Glossophora sp	Big Rat Island Lagoon
		Laminariales	Alariaceae	*Ecklonia radiata* (Turn.)J.Ag.[a]	Whitford Beach
Rhodophyta	Rhodophyceae (subclass Florideae)	Ceramiales	Rhodomelaceae	*Laurencia filiformis* (C.Ag.) Montagne	Yanchep
				Laurencia filiformis f *filiformis* Saito & Womersley	Point Peron
				Laurencia filiformis f *heteroclada* (Harvey) Saito & Womersley	Cottesloe; Lancelin; Shoalwater Bay; Hamelin Bay
				Laurencia majuscula (Harvey) Lucas	Woodman Point
				Choudria sp	Rat Island, Houtman Abrolhos
				Vidalia spiralis Lamouroux[b]	Yanchep
		Gigartinales	Plocamiaceae	*Plocamium mertensii* (Grev.) Harvey	Carnac Island; Hamelin Bay; Lancelin
				Plocamium preissianum Sonder	Augusta
				Plocamium sp	Rottnest
				Plocamium sp	Cottesloe
				Plocamium sp	Big Rat Island
			Phacelocarpaceae	*Phacelocarpus labillardieri* (Mertens) J.Ag.	Cosy Corner
			Hypneaceae	*Hypnea* sp[c]	Quobba Lagoon
		Nemalionales	Bonnemaisoniaceae	*Delisea* sp	Redgate Beach, Hamelin Bay

* Specimen samples of the algae, except those marked a, b, c, have been lodged with the Department of Botany, The University of Western Australia.

The order Dictyotales is one of the most distinct of the Phaeophyta and considerable work on the metabolites produced by members of this order has been published. From WA two species have been examined. A *Glossophora* sp yielded the macrocyclic dialdehyde (**68**) (Arrowsmith 1983) and *Dictyota furcellata* the new dolastane diterpene (**69**) (Dunlop *et al* 1989). The cosmopolitan and sub-tropical genus *Dictyota* has been shown to produce a number of biologically active diterpenes based on the dolastane ring system.

The ability of marine algae to accumulate substantial concentration of arsenic has been known for some time. In efforts to determine the source of arsenic in marine fauna from the unpolluted coastal waters of WA, algae were surveyed and the brown kelp, *Ecklonia radiata* (Order: Laminariales; Family: Alariaceae) was found to contain arsenic at a concentration of 10 mg kg^{-1} (wet weight). Further studies revealed that the arsenic was present in the form of the arseno ribofuranosides (**49**, **70**, **71**) (Edmonds & Francesconi 1983). It is possible that these compounds represent a mode of entry for arsenic into the marine food chain and could well be the source of arsenobetaine (**48**) in marine fauna.

The red algae, Rhodophyta, have many delicate and intricate species. Australasia, with at least 1 100 species and 370 genera, contains a greater diversity of red algae than any other comparably sized region on earth (Kraft & Woelkerling 1981). Chemical studies have revealed them to be a rich source of halogenated terpenes and acetogenins. Particularly prolific in yielding interesting secondary metabolites are the genera *Laurencia* and *Plocamium*.

Laurencia (Order: Ceramiales; Family: Rhodomelaceae) is a common genus on southern Australian coasts and includes numerous species which are often ecologically important (Saito and Womersley 1974). Most species are clearly defined but *L. filiformis* includes three main forms, which have been named *filiformis*, *heteroclada* and *dendritica*, with intergrades between them, and intergrades from it to the related species *L. arbuscula* and *L. tasmanica*. From *L. filiformis* f. *filiformis* we have isolated aplysistatin (**72**) and 6β-hydroxy-aplysistatin (**73**) (Capon *et al* 1981d)

Because of the ecological importance of this genus we have also examined the constituents of samples of *L. filiformis* f. *heteroclada* collected at four different points along the Western Australian coast; Hamelin Bay, Shoalwater Bay (*ca* 50 km south of Perth), Cottesloe Beach (Perth) and Lancelin. In each case the alga was found to elaborate known laurene sesquiterpenes as the major metabolites. Whereas the sample from Hamelin Bay contained only allolaurentirol (**74**), those from Lancelin and Cottesloe Beach in addition produced laurenisol (**75**) and bromolaurenisol (**76**) respectively. In contrast, the Shoalwater Bay sample yielded (**75**), (**76**), isolaurentirol (**77**), filiformin (**78**) and (-)-α-bromocuparene (**79**) (Capon *et al* 1988).

Previous work on two collections of *L. filiformis* f. *heteroclada* from the Eastern States has shown that both contained sesquiterpenes based on the laurene skeleton but in addition one sample contained heterocladol, a halogenated selinane sesquiterpene (Wells 1979). A sample of *L. filiformis* from Lancelin contained compounds (**80**, **81**) based on the selinane skeleton (Brennan & Erickson 1982). These results suggest that the f. *heteroclada*, in terms of the sesquiterpene metabolites it produces, is clearly distinct from the f. *filiformis*. It seems likely that the third form of the *L. filiformis* complex, f. *dendritica*, is also distinct and it is the form which produces prepacifenol, a chamigrene sesquiterpene. In this context it is interesting to note that *L. tasmanica* which can be regarded as an extreme form of the *L. filiformis* complex bordering f. *dendritica* (Saito & Womersley 1974) has been shown to produce a similar compound (Sims *et al* 1973).

In contrast to the *L. filiformis* "complex", *L. majuscula* is a distinctive species widely distributed along the southern Australian coast including Tasmania (Saito & Womersley 1974). *L. majuscula*, collected from Woodmans Point (*ca* 30 km south of Perth), was found to elaborate the known chamigrene sesquiterpenes obtusane (**82**), obtusol (**83**), elatol (**84**) and isoobtusol (**85**). Although these compounds have been isolated from various *Laurencia* species they have not been reported before from *L. majuscula* and differ from the chamigrenes present in the Mediterranean and Japanese varieties (Capon *et al* 1988).

Two other members of the Rhodomelaceae family have been investigated. An undetermined *Chondria* sp, found attached to coral (*Acropora* sp) near Rat Island, in the Eastern Group of Houtman Abrolhos, was observed to rapidly decompose on exposure to air, such that the filamentous alga took on a 'paste' like consistency. In this form the alga was particularly unpleasant to handle, causing a lingering 'tingling' sensation, and emitted a sulphurous odour. Extraction returned a low yield of lipophilic material (0.06%), from which a mono methyl ether of reductic acid (**86**) was recovered (Capon 1982). Reductic acid has been reported as a hydrolysis product of alginic acid (a natural product found in Phaeophyta), L-ascorbic acid and *Laminaria* powder (Aso 1939). Methylation of the product obtained on hydrolysis of the latter afforded a mono methyl ether with the same melting point as **86**. The acidic nature of the decomposed alga (*ca* pH 5) supports speculation that **86** is derived from reductic acid *via* acid catalysed methylation (during extraction with dichloromethane: methanol [1:1], and furthermore that reductic acid is itself a degradation product.

Crude extracts of *Vidalia spiralis* exhibited hypotensive activity. Although the new compound (**87**) was isolated it was not the active principle (Kauzlauskas *et al* 1982c).

The Gigartinales is a large order which is particularly well represented in Australia (*ca* 200 species) (Kraft & Woelhering 1981). The most widely studied genus of this group is *Plocamium* which occurs frequently along the WA coast. A large number of alicyclic and acyclic, brominated and chlorinated, monoterpenes have been isolated from a variety of *Plocamium* spp, collected at geographically distant locations *ie* Antarctica, the British and Californian coasts and the coast of Australia (Capon 1982). On several occasions the same or similar compounds have been reported as constituents of the lipid extract of the digestive gland of sea-hares (*Aplysia* spp), which are known to graze on algae, accumulating toxic secondary metabolites for defensive purposes. The antibacterial properties of *Plocamium* extracts have been known for some time and with the advent of more sophisticated isolation, purification and identification techniques, together with more specific bioassays, it has been possible to identify these unusual, and often unstable, natural products.

During our investigations of local *Plocamium* spp we found that the abundant red alga *P. mertensii*, collected off Perth contained the known rearranged alicyclic monoterpene, plocamadiene-A (**88**), as the only isolatable secondary metabolite (Capon *et al* 1984). At this time, **88** had been reported from a British collection of *P. cartilagineum*, where it was isolated as an oil, and from *P. cartilagineum* collected off the east coast of Australia (Capon 1982). As a result of the latter isolation plocamadiene-A (**88**) was found to possess a novel pharmacological activity "[It] produces a spastic syndrome in mice which persists for several days but is ultimately reversible" (Spence & Wells 1978). The same compound was present in a sample collected at Lancelin together with the related compound (**89**) and the acyclic monoterpene (**90**). A third sample from Hamelin Bay yielded similar compounds (**91-93**) (Bestow 1981). All three samples also contained the glycerylglucose floridoside (**94**).

A collection of *Plocamium preissianum* from Augusta was found to contain a complex mixture of polyhalogenated monoterpenes from which two acyclic compounds **95** and **96** were isolated (as a 1:1 mixture) (Capon 1982). Both **95** and **96** are known metabolites of *P. cartilagineum*, Californian specimens of which were found to elaborate polyhalogenated acyclic monoterpenes whereas British, Spanish and Antarctic speciments yielded alicyclic halogenated monoterpenes (Capon 1982). An unidentified *Plocamium* sp, collected from the beachwash on Rottnest Island, contained the known alicyclic bromotrichloromonoterpene mertensene (**97**) (Capon *et al* 1984). Mertensene (**97**) had previously been reported as the major metabolite of *P. mertensii*, collected at Cape Jervis in South Australia but had been assigned the wrong structure (Norton *et al* 1977). From a local species of *Plocamium*, collected along Cottesloe Beach near Perth, we isolated the known bromo analogue of **89**, bromoviolacene-1 (**98**) (Capon 1982) which is also present in a *Plocamium* sp from Big Rat Island together with plocamadiene-A (**88**) and the acyclic monoterpene (**99**) (Arrowsmith 1983).

A collection of *Phacelocarpus labillardieri* from Cosy Corner yielded (Capon *et al* 1988) compounds with structure similar to **100** and analogues reported from the same species collected in South Australia and Tasmania (Kauzlaskas *et al* 1982d).

A methanol extract of *Hypnea valentiae* collected at Quobba Lagoon produced pronounced muscle relaxation and hypothermia in mice and also blocked poly- and monosynaptic reflexes. The compound responsible for all these activities after purification was shown to be the unique iodinated nucleoside (**101**). A minor component of the extract was shown to be the isomer (**102**) which showed lower biological activity than (**101**) (Kauzlaskas *et al* 1983).

The only member of the family Bonnemaisoniaceae examined was a *Delisea* sp found near Hamelin Bay. The compounds obtained (**103-108**) had previously been isolated from *D. fimbriata* collected near Sydney (Capon 1982).

Marine Cyanophytes

Blue-green algal mats and stromatolites are the dominant autotrophs of the hypersaline waters of Shark Bay, Western Australia. Algal mats extend from shallow subtidal depths (*ca* 4 m) to an elevation of *ca* 2 m above low water level and can be differentiated into four basic types and three intergradational types that can be distinguished on the basis of surface texture and colour (Logan *et al* 1974). Each mat type is colonized by a dominant cyanophyte. Three of the seven types of algal mats (Table 4) were examined for the presence of lipophilic metabolites. Extraction of the freeze-dried algal mats with methylene chloride: methanol afforded, in all but one case, a white translucent polymer. Chemical studies showed it to be poly-β-hydroxybutyrate (PHB) (**109**) and either a heteropolymer containing units of β-hydroxybutyric and β-hydroxypentanoic acids (**110**) or an inseparable mixture of PHB and poly-β-hydroxypentanoate (PHV) (Capon *et al* 1983). A similar mixture was obtained from an *Aphanothece* sp from Lake Joondalup. The results obtained (Table 3) establish the presence of polyesters in cyanobacteria growing in vastly different environments, viz. a permanent freshwater lake and a variable hypersaline intertidal zone. It also seems clear that one of the polyesters is PHB, a chiral polymer which normally occurs as hydrophobic granules in the cells of a wide variety of bacteria. Only a few reports of its presence in cyanobacteria have appeared. The occurrence and identification of PHB in the blue-green alga, *Chlorogloea fritschii*, after growth in the presence of acetate has been reported (Carr 1966). No PHB could be detected after growth of *C. fritschii* on an autotrophic medium in the absence of acetate, or growth of *Anabaena variabilis* in the presence or absence of acetate. PHB has been detected also in an *Oscillatoria* sp (Moore 1981).

Table 4

Polyesters from Cyanobacteria

Locality	Form	Cyanophyte	Polymer yield (pentanoate-butanoate)
Lake Joonadalup Perth	metaphyton	*Aphanothece* sp.	0.2%* (2:1)
Hutchison Bay Shark Bay	pustular mat	*Microcoleus* sp.	0.02%† (n.d.)
Hamelin Pool Shark Bay	smooth mat	*Schizothrix calcicola* (C.Agardh)Gomont.§ *Symploca laete-viridis*, Gomont. *Scytonema* sp.	00.3%† (1:1)
Hamelin Pool Shark Bay	tufted mat	*Lyngbya aestuarii* Gomont. *Microcoleus chthonoplastes* Thur.	0.03%† (1:4)
Hamelin Pool	pustular mat	*Entophysalis deusta* Drouet and Daly	0

* Yield based on wet wt
† Yield based on freeze dried wt of algal mat
§ Dominant cyanophyte

PHB and PHV are being evaluated for industrial use. Both are aliphatic polyesters of high molecular weight and stereoregularity and as such are good sources of chiral monomers. They are biodegradable in soil, can be plasticized and take glass-fibre filling very well. Their production from bacterial sources does not appear to be competitive with oil-based thermoplastics yet. The occurrence of these polymers in cyanophytes, which are autotrophic, is of some significance. Large scale cultivation of the cyanophytes dominating the hypersaline environments of Shark Bay may allow the production of these polymers at competitive costs.

Sea Grasses

Amphibolis antarctica and *Posidonia australis* are the major sea grasses of Shark Bay, Western Australia (Walker *et al* 1988). Meadows of these grasses dominate the metahaline regions of the Bay establishing complex floral and faunal communities within monospecific stands of grass. The grasses are rarely directly grazed but form a detrital energy chain *via* the shedding and subsequent settling of leaves (Walker & McComb 1985). An ongoing study of the organic geochemistry of the sediments of Shark Bay required knowledge of the input of hydrocarbons from sea grass leaves. *Posidonia australis* had been examined in this context but no study existed for *A. antarctica* which provides the larger biomass of these sea grasses in Shark Bay (Walker *et al* 1988). Examination by GC/MS of the hydrocarbons from the leaves of *A. antarctica* showed the presence of *n*-alkanes (C_{17}-C_{25}, odd number predominance) and a diterpene hydrocarbon. Extraction of a large sample of leaves, followed by silicic acid and alumina chromatography of the crude extract, yielded a colourless oil, (0.0002% of fresh wt) to which structure (**111**) was assigned on the spectroscopic evidence (Dunlop 1985). Collections of *A. antarctica* from near Perth contained not only (**111**) but also the known diterpene hydrocarbons sandaracopimaradiene (**112**) and isopimaradiene (**113**).

Analysis of individual heads of leaves of *A. antarctica* from Shark Bay showed: (a) that *n*-alkanes are concentrated in juvenile leaves and diminish as the leaf ages; and (b) that (**111**), while not detected in juvenile leaves, increases with leaf age and persists in leaves which have become detritus. It is possible during high physical energy conditions, such as cyclones, that whole *Amphibolis* beds may be disturbed and, subsequently, buried thereby contributing both *n*-hydrocarbons and diterpenes to the sediment hydrocarbon profile. In samples from near Perth, the same distribution of *n*-alkanes and all three diterpenes is observed. Epiphytes on the leaves contribute a significant proportion of *n*-heptadecane.

Sediments

The physical and biological environments of Shark Bay have been the target of considerable studies (Logan & Cebulski 1970). A stable salinity gradient has been defined and this ranges from oceanic waters in the north, through a metahaline phase (Hopeless Reach and Freycinet Basin) to hypersaline water in Hamelin Bay. Associated with this there are three biotic communities with bivalves dominating the embayment plain of the oceanic environment with only sparse flora, sea grass cover in the metahaline and sparse algal flora and *Fragum* community in the hypersaline basins. The chemical assemblage of sediment hydrocarbons along the salinity gradient may be classified into two distinct chemogeographic types. Firstly, oceanic sediments contain *n*-alkanes and a suite of highly branched and branched/cyclic C_{25} alkenes. Hypersaline sediments are characterised by a high relative abundance of a $C_{25}H_{50}$ alkene (**114**) together with an analogous $C_{20}H_{40}$ alkene (**115**) and its parent $C_{20}H_{42}$ alkane (2,6,10-trimethyl-7-(3-methylbutyl)-dodecane) (**116**). A pair of alkanes $C_{21}H_{44}$ and $C_{22}H_{46}$ increase in concentration and relative abundance with depth. The hydrocarbons of the hypersaline basins are found in only trace amounts in oceanic sediments. These chemical signals are overlain by further input indicative of the immediate biotic community. The two chemically distinct regions are not aligned with the macrobiotic sea grass communities and the detailed hydrocarbon chemistry of the sea grass sediments indicates that the origin of the oceanic and hypersaline alkenes are derived from another undisclosed source (Dunlop & Jefferies 1985).

To the north of Shark Bay lies the land-locked marine sedimentary basin Lake McLeod. In the north-west of the basin, hypersaline ponds are maintained via the influx of marine waters through cavernous limestone and efflux away from the vents downslope to the east. Evaporation provides present day sequences of carbonate and gypsum (Logan 1987). During a preliminary examination of the organic geochemistry of these sequences, the compounds (**115**) and (**116**) were observed as major components of the carbonate mud hydrocarbons. At Cygnet Pond, a south to north transect from the pond to dry exposed shore demonstrated that the carbonate mud of the pond contained the alkene (**115**) while those of exposed carbonate contained the alkane (**116**). The presence of the alkene in pond sediment was not associated with macroscopic biota (*eg* the green algae *Cladophora* or the aquatic angiosperm *Ruppia* sp.). Likewise the alkane was not derived from cyanobacterial mats which cover the shore and are frequently buried (Dunlop unpublished results).

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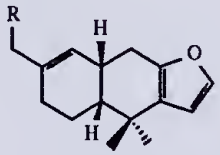
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APPENDIX Compounds isolated from Western Australian marine fauna and flora*

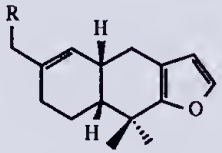
Porifera

Dysideidae



(1) R =H (0.13%) *Dysidea sp;Undet.genus*

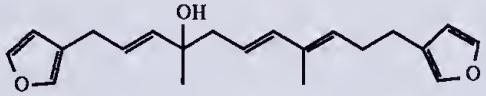
(2) R= SAc(0.005%) *Dysidea sp*



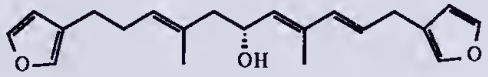
(3) R = H (0.13%) *Dysidea sp; Undet.genus*

(4) R = SAc(0.36%) *Dysidea sp*

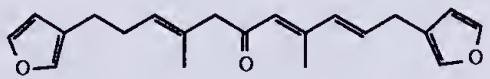
Spongiidae



(5) (1%) *Spongia sp*

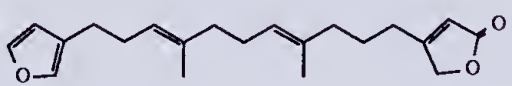


(6) (0.6%) *Leiosella sp*

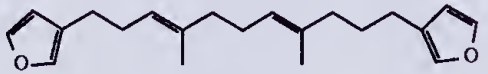


(7) (0.2%) *Leiosella sp*

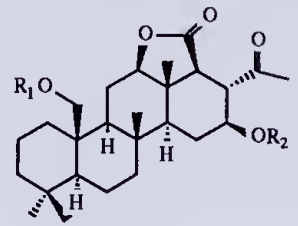
*Porifera and Algae are listed according to families.For each compound a text number is given together with the source organism and,where available,yields expressed as percentage of the dry biomass.



(8) (1.35%) *Lendelfeldia sp*



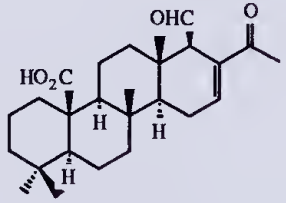
(9) (0.33%) *Lendelfeldia sp*



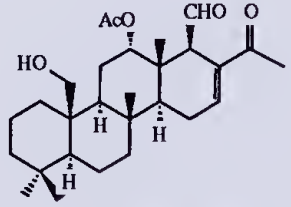
Lendelfeldia sp

(10) R_1 = Ac; R_2 = H

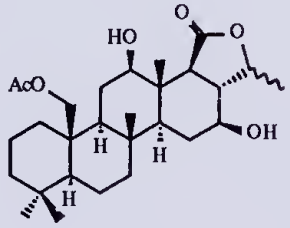
(11) R_1 = H ; R_2 = H



(12) *Lendenfeldia sp*

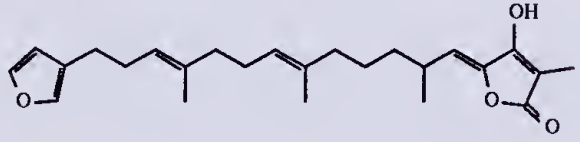


(13) *Lendefeldia sp*

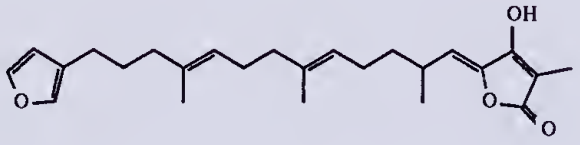


(14) *Lendefeldia sp*

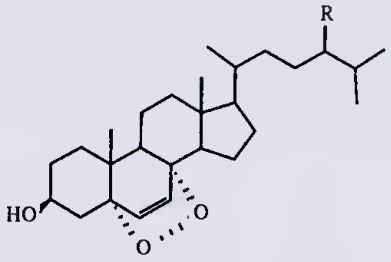
Thorectidae



(15) (0.02%) *Ircinia sp*



(16) (0.02%) *Ircinia sp*

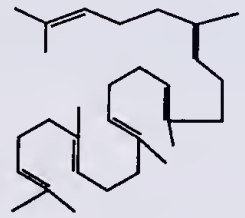


Ircinia sp

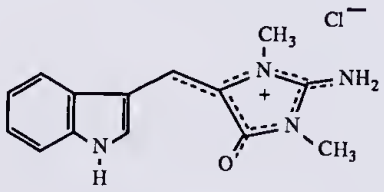
(17) R = H

(18) R = CH_3

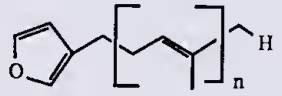
(19) R = CH_2CH_3



(20) (0.07%) *Ircinia sp*



(24) (0.2%) *Thorectandra sp*

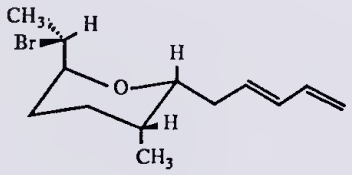


(21) n = 6 (0.12%) *Ircinia sp;* (0.2%) *Thorectandra sp* (0.2%)

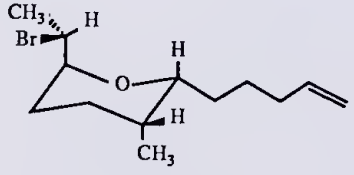
(22) n = 8 (0.2%) *Ircinia sp*

(23) n = 10 (0.08%) *Ircinia sp*

Haliclonidae

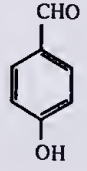


(25) (0.4%) *Haliclona sp*

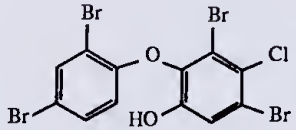


(26) (0.2%) *Haliclona sp*

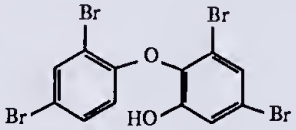
Callyspongidae



(27) (0.05%) *Dactylia sp*

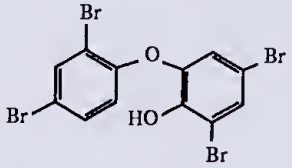


(28) (1.3%) *Undet.genus*



(29) (1.2%) *Undet.genus*

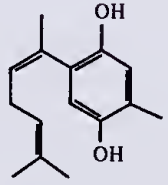
(2.0%) *New genus*



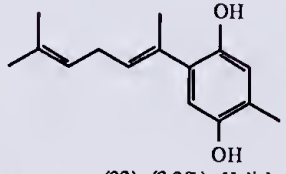
(30) (0.05%) *Undet.genus*

(0.05%) *New genus*

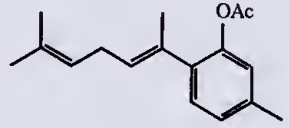
Halichondriidae



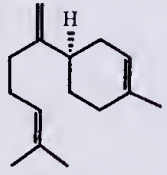
(31) (3.1%) *Halichondria sp*



(32) (3.2%) *Halichondria sp*

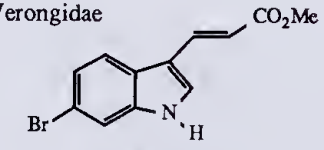


(33) (0.4%) *Halichondria sp*



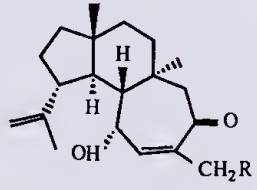
(34) (4.5%) *Halichondria sp*

Verongidae



(35) *Iotrochota sp*

Desmoxiidae

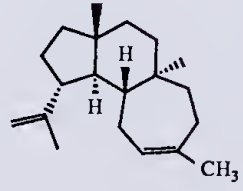


Higginsia sp

(36) R = CH_2OH

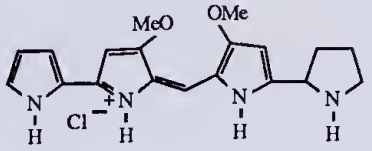
(37) R = CH_2OAc

(38) R = CH_3



(39) *Higginsia sp*

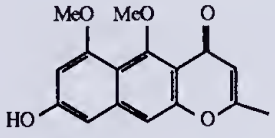
Compound Ascidian



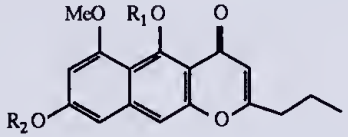
and (40)

Br⁻

Echinoderms

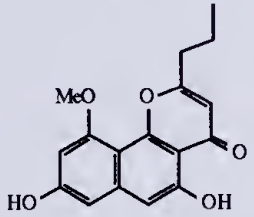


(41) *Comantheria solaris*

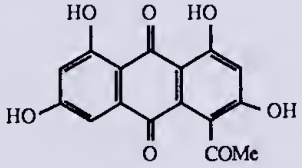


(42) R_1=Me, R_2=H *Comantheria solaris*

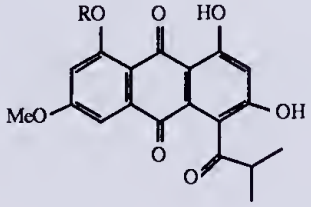
(43) R_1=R_2=H *Comantheria solaris*



(44) *Comantheria solaris*



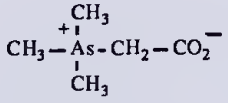
(45) *Coumatula solaris;*



(46) R = Me *Coumatula solaris; Comatula rotalaria*

(47) R = H *Comatula rotalaria*

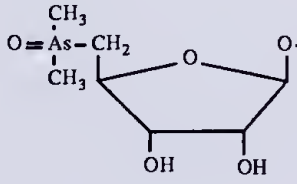
Others



(48) *Panulirus cygnus*

Carcharinus obscurus

Sillago bassensis



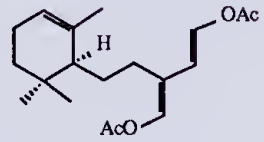
Tridacna maxima

(49) R = OH

(50) R = OSO_3H

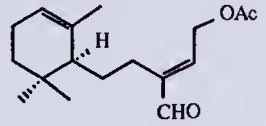
Algae

Caulerpaceae



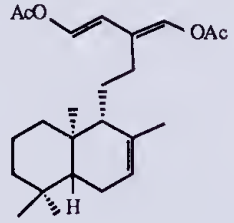
(51) (0.05%)

Caulerpa flexilis var muellerii

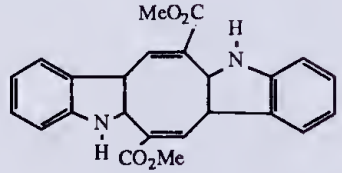


(52) (0.005%)

Caulerpa flexilis var muellerii



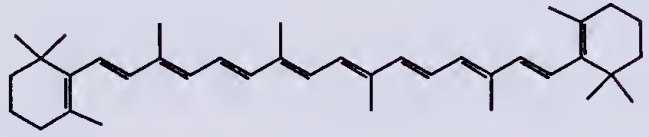
(53) (0.4%) *Caulerpa trifaria*



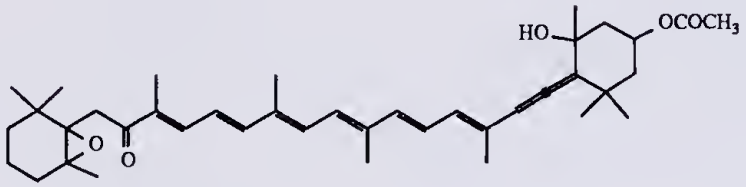
(54) (0.003%) *Caulerpa peltata*

(0.003%) *Caulerpa racemosa*

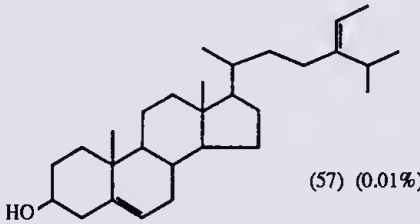
Cystoseiraceae



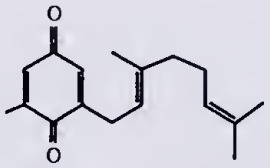
(55) (0.007%) *Cystophora sp*



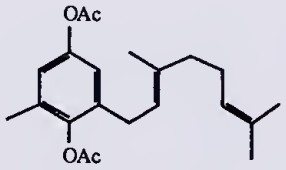
(56) (0.09%) *Cystophora sp*



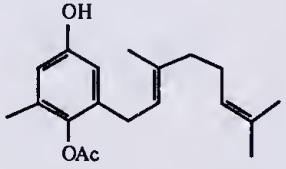
(57) (0.01%) *Cystophora sp*



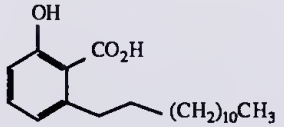
(58) (0.03%) *Cystophora sp*



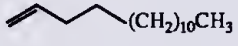
(59) (0.03%) *Cystophora sp*



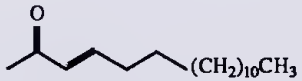
(60) (0.07%) *Cystophora sp*



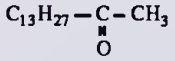
(61) (0.13%)
Caulocystis uvifera



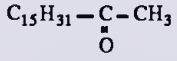
(62) (0.13%)
Caulocystis uvifera



(63) (0.04%)
Caulocystis uvifera

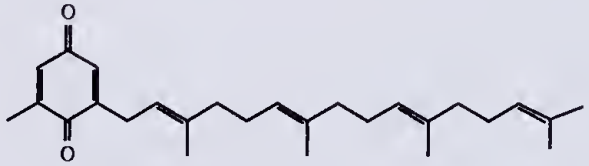


(64) (0.005%) *Caulocystis uvifera*

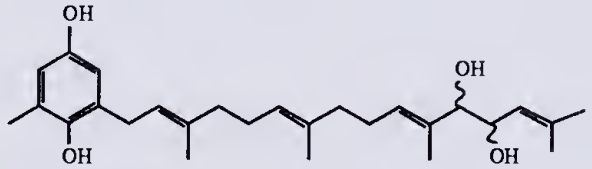


(65) (0.002%) *Caulocystis uvifera*

Sargassaceae

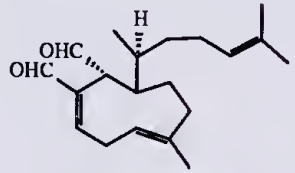


(66) (0.019%) *Sargassum sp*

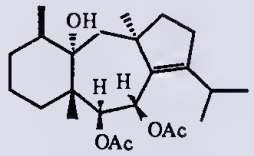


(67) (0.18%) *Sargassum sp*

Dictyotaceae

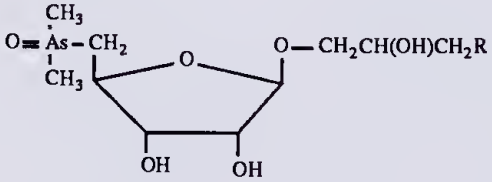


(68) (0.07%) *Glossophora sp*



(69) *Dictyota furcellata*

Alariaceae

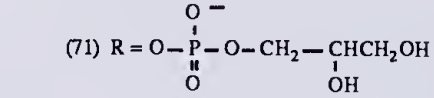


Ecklonia radiata

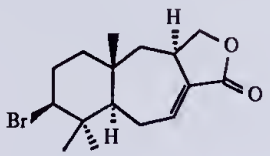
(49) R = OH

(50) R = OSO_3H

(70) R = SO_3H

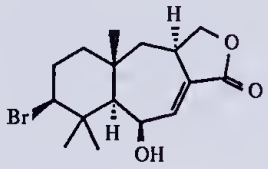
(71) R = 

Rhodomelaceae



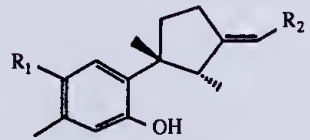
(72) (0.4%)

Laurencia filiformis f filiformis

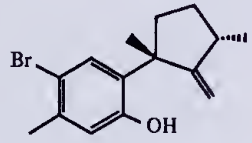


(73) (1.6%)

Laurencia filiformis f filiformis

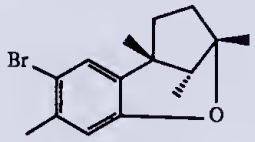


Laurencia filiformis f heteroclada



(77)

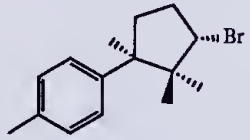
Laurencia filiformis f heteroclada



(78)

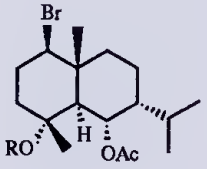
Laurencia filiformis f heteroclada

	R_1	R_2
(74)	Br	H
(75)	H	Br
(76)	Br	Br



(79)

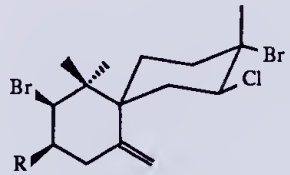
Laurencia filiformis f heteroclada



Laurencia filiformis

(80) R = H

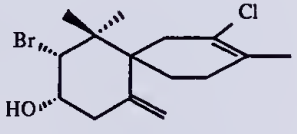
(81) R = Ac



Laurencia majuscula

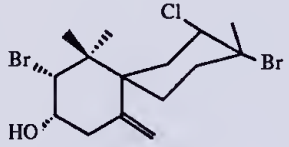
(82) (0.02%) R =H

(83) (1.2%) R = OH



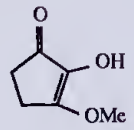
Laurencia majuscula

(84) (0.4%)

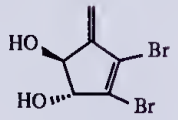


Laurencia majuscula

(85) (0.05%)

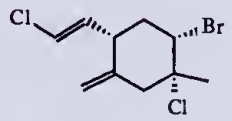


(86) (0.06%) *Chondria sp*

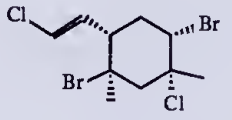


(87) *Vidalia spiralis*

Plocamiaceae

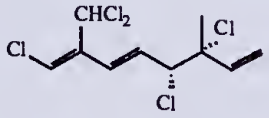


(88) (0.4%) *Plocamium mertensii*

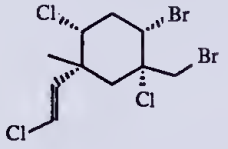


(89) (0.4%) *Plocamium mertensii*

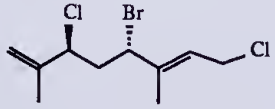
Plocamium ssp



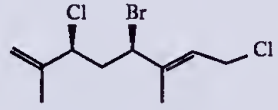
(90) (0.7%) *Plocamium mertensii*



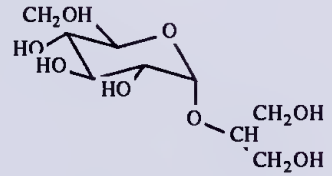
(91) (0.04%) *Plocamium mertensii*



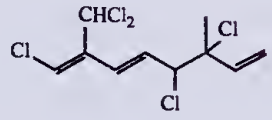
(92) (0.02%) *Plocamium mertensii*



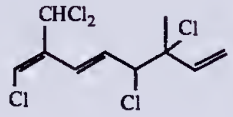
(93) (0.02%) *Plocamium mertensii*



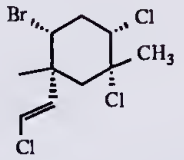
(94) (0.06%) *Plocamium mertensii*



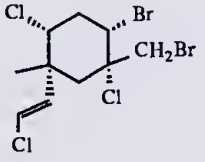
(95) *Plocamium preissianum*



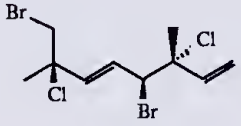
(96) *Plocamium preissianum*



(97) (0.05%) *Plocamium sp*

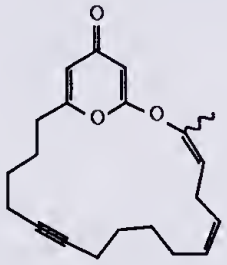


(98) *Plocamium sp*



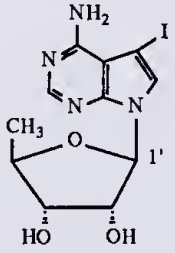
(99) *Plocamium sp*

Sphaerococcaceae



(100) *Phacelocarpus labillardieri*

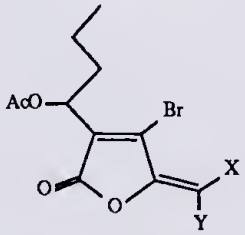
Hypneaceae



(101) 1' β-- Hypnea valendiae

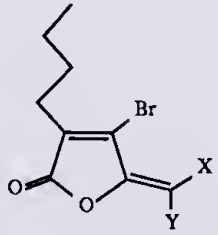
(102) 1' α--Hypnea valendiae

Bonnemaisoniaceae



Delisea sp

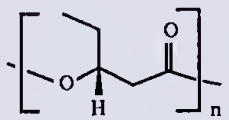
	X	Y
(103) (0.74%)	Br	H
(104) (0.74%)	H	Br
(105) (0.02%)	Br	Br



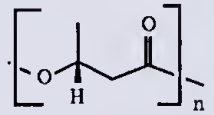
Delisea sp

	X	Y
(106) (0.06%)	Br	H
(107) (0.06%)	H	Br
(108) (0.10%)	Br	Br

Cyanophyta

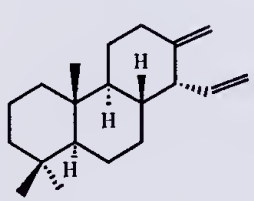


(109) blue-green algae

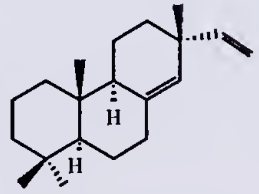


(110) blue-green algae

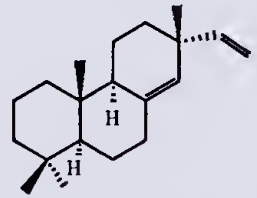
Seagrass



(111) *Amphibolis antarctica*

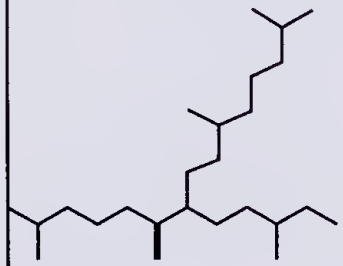


(112) *Amphibolis antarctica*

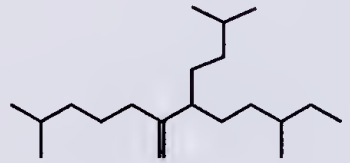


(113) *Amphibolis antarctica*

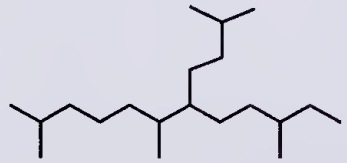
Sediment Hydrocarbons



(114)



(115)



(116)

Journal of the Royal Society of Western Australia, 72 (4), 1990, 109-121

Wetlands of the Darling System, Southwestern Australia: a descriptive classification using vegetation pattern and form

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Abstract

A classification is proposed for wetlands of the Darling System based on the scale of wetland vegetation complexes; extent of vegetation cover over the wetland; internal organization of vegetation in plan; vegetation structure; and details of the floristic/structural components. Vegetation cover is divided into 3 intergradational classes: peripheral, mosaic and complete. Complexity of wetland vegetation is divided into 3 classes: homogeneous, zoned and heterogeneous. The combination of cover and internal organization results in the recognition of 9 basic wetland vegetation categories: periform, paniform, latiform, zoniform, gradiform, concentriform, bacataform, heteroform, and maculiform. These terms form the primary part of a binary terminology, which forms the core of the classification. Established structural terms are adopted to describe the structure of wetland vegetation, and this forms the second part of the binary terminology. Scale terms are added as adjectival qualifiers, and details of floristics and structure in combination may be added as an inventory to the main binary system. Thus this approach provides a systematic way to describe and compile an inventory of wetland vegetation units. The classification provides a conceptual picture of the wetland vegetation, and the diversity and complexity of vegetation of specific wetlands then become obvious. It also allows for wetlands to be classified and thus easily mapped. The classification categories presented in this paper may be used, if required, as qualifiers to existing wetland classifications.

Introduction

A range of classification schemes have been developed for terrestrial vegetation, variably emphazing one or more of the structural, physiognomic, functional and compositional features of vegetation appropriate to the scale at which the classification is required (Braun-Blanquet 1932, Raunkiaer 1934, Whittaker 1962, Specht 1981). These schemes have been applied only with partial success to wetland vegetation. Indeed, workers in wetland settings have tended to develop their own classifications for vegetation to encompass a range of other attributes, such as plant-water relationships, that they have considered to be important (Tansley 1939, Martin *et al* 1953, den Hartog & Segal 1964, Gore 1983).

Developing a classification for vegetation *within* a wetland is difficult because the vegetation ranges from simple to complex in several ways: in size, it may range from small scale to regionally extensive units; in structure, it may contain a mix of forests, heaths, grasslands, etc; and in organization, it may be simple, or zoned, or composed of mosaics. Mosaics may reflect variation in community history, or variation and gradients in topography, soils, water availability, and other edaphic factors. Extensive, "simple" (structurally and compositionally homogeneous) wetland vegetation, on the other hand, may reflect underlying uniform environmental conditions. These are some of the aspects of wetland vegetation which multiply the difficulties already inherent in their classification.

It is our view, however, that wetland vegetation can be classified simply, provided that some fundamental attributes of wetlands are addressed first. Wetlands, particularly basins, tend to be discrete areas, and so wetland vegetation lends itself to categorization by scale, internal floristic and structural organization as well as degree of complexity. This paper proposes a classification of wetland vegetation based on these organizational and scale aspects of the vegetation. The classification has been designed specifically for the basin wetland vegetation of the Darling System of southwestern Australia, because it was developed on a data base from that area. However, the principles and terminology of the classification should have more widespread applicability in Australia and elsewhere.

Literature review

The classification of wetland vegetation has always been a particularly difficult task due to the large number of causal factors and relationships involved. As a result there have developed a number of systems with various objectives and emphases. The major objectives in vegetation classification, as summarized by Whittaker (1962, 1980) and Anderson (1981), are to: document geographic distribution; document succession and dynamic change within communities; compare stands of vegetation and analyse their intergradation; and correlate or show a causal relationship between edaphic conditions and plant characteristics.

Criteria for vegetation classifications have been drawn from all aspects of plant study. These include: physiognomy, structure, life form, function, composition (floristics), successional stage, habitat, and history (Fosberg 1970). Several of these criteria are often used within a hierarchical framework to increase the divisions within the classification. The most frequently used criteria are physiognomy, structure, life form, and composition. It is inherently difficult to use history as a criterion in vegetation classification, and for philosophical and practical reasons this has not been attempted in most classifications. Generally, workers on wetland vegetation have utilized established classification systems drawn from the above, sometimes with added emphasis on water-related features. A brief review of these classification systems as they have been applied to wetland vegetation is provided here.

Wetland vegetation has most frequently been categorised on life form and physiognomy (*eg* trees, reeds, mosses, *etc*), in combination with gross compositional features. The products of life forms, or of specific plant groups (*eg* peat accumulation from mosses) also have been incorporated into the classification of wetlands. As a result there has developed a range of terms such as bog, fen, marsh, swamp, carr, meadow. These categories commonly are viewed as first order and consequently form the basis of many classifications in Europe and Africa (Tansley 1939, Ratcliffe 1964, Zoltai & Pollett 1983, Gore 1983, Ruuhijarvi 1983, Zahran 1977). These vegetation categories may also relate to plant function and ecological factors, essentially reflecting the variable response of plants to differences in substrate composition, nutrient status, and water regime. Three examples illustrate these relationships. Fen formations are permanently waterlogged, have peat substrates, a high nutrient status, and are composed of hypnoid mosses, tall graminoids, and herbaceous plants. Similarly, bogs have a permanently waterlogged peat substrate, but with a low nutrient status, and are composed of mosses (predominatly *Sphagnum*), low graminoids and dwarf shrubs. In contrast, swamp formation refers to macrophyte woody, herbaceous or graminoid wetland vegetation that inhabits waterlogged soils. Swamp vegetation commonly is divided into two diagnostic structural types, reed swamp and woodland swamp (Tansley 1939, Ivanov 1981, Gore 1983, Denny 1985). However, many of these wetland terms have been used synonymously, and some terms have been used to describe widely different ecological settings (*eg* marshes, swamps, meadows; see review in Semeniuk 1987).

The spatial arrangement of vegetation, or structure, has been generally used only in a restricted manner (*ie* height classification and spacing). Aspects of physiognomy, such as branching habit, and geometry and configuration of crown and roots, may be too complex for use in wetland vegetation analysis and classification. Traditionally, the main features which have been used in structural classifications are life form and height, and less frequently, foliage projective cover (Specht 1981). These features have been used at the second stage of classification by many authors (Braun-Blanquet 1932, Ruuhijarvi 1983, Campbell 1983, Pisano 1983). Vegetation structure also has been used with other features, most commonly floristics and plant functional characteristics. However, the successful combined use of structural and compositional features has been achieved in classifying vegetation other than in wetlands, where only limited attempts at such an approach have been made.

Criteria of life form are designed to reflect the variety of adaptations made by wetland and aquatic plants to the prevailing environmental conditions, and it is in this arena that the main ideas on wetland vegetation have originated. Several major classifications recognize adaptations by plants to unfavourable seasons, substrate, or water (Raunkiaer 1937, den Hartog & Segal 1964). For instance, the position of perennating buds in vascular plants relative to soil level has been a feature used in classification; in this example, there are hydrophytes (plants which grow in, or at the surface of water), helophytes (plants which grow in seasonally or permanently waterlogged soils), phanerophytes (perennating buds >2 m above soil) and chamaephytes (perennating buds 0-25 cm above soil). Amendments to the definition of hydrophytes and helophytes have been made by Braun-Blanquet (1932), Cook (1968), Spence (1964), Cook *et al* (1974), and Denny (1985), amongst others. The term macrophyte denotes those plants with vegetative parts that are permanently or seasonally submerged in, or emerge from fresh water, or float on the water surface (Cook *et al* 1974), and is commonly used, with a qualifier, to describe the relationship of plants to the water habitat *eg* free floating, submerged, emergent, floating leaved (Tansley 1939, Spence 1964, Golet & Larson 1976, van der Valk 1981, Junk 1983, Denny 1985).

Functional criteria, which have been used in classifying wetland vegetation (either at the level of individual plants or of whole biocoenoses), are seed germination requirements (van der Valk 1981), xeromorphy (Cowardin *et al* 1979), and salt adaptive strategies (Scholander *et al* 1962). Such functional criteria are particularly suitable for examining vegetation with respect to a hydrological gradient. However, in comparative wetland studies where there is a need for primary vegetation classification, an overemphasis on functional criteria could restrict the use of other primary information, as certain life forms may predominate in particular wetland conditions.

Some classifications for purposes of further subdivision have depended then on floristic composition (genera and species). Practitioners of floristic classification use compositional data in a variety of ways, principally as: dominant species approach (Tansley 1939, Thompson & Hamilton 1983); qualitative comparative approach (Braun-Blanquet - Zurich Montpellier School; Moore 1962, Poore 1955 a,b,c, Chapman 1977); and numerical comparative classifications (Bridgewater 1981, Backshall & Bridgewater 1981). Although there is variation between the 3 approaches and the theoretical structure upon which they are based, resulting in the identification of distinct classes of

vegetation, these approaches result in similar vegetation terminology (*eg* the *Shorea alluda-Litsea parastemon* community, Anderson 1981; the *Spartina* community, Beeftink 1977; and, in Australia, the *Juncetum krausii* association, Bridgewater 1981). The emphasis in these classifications is on communities and as such they do not convey information on the vegetation structure and organization, aspects which can be major features of the vegetation patterns in wetlands.

Successional stage in wetland vegetation is of major importance and also has been used as the basis of classification (Tansley 1939, Van der Valk 1981, Denny 1985). However, as Gleason (1926) states "vegetation of an area is fluctuating and fortuitous". For example, in some areas seres have been documented as climax communities, whereas in other areas the vegetation has maintained an equilibrium which does not conform to the established sere. With constantly changing environmental conditions, both natural and human-induced, wetland vegetation is best classified on other criteria within a framework which does not embody any conclusions about dynamic processes.

Habitat classification has been used as a basis for describing and classifying variable patterns of tropical littoral vegetation (Semeniuk & Wurm 1987). Because geomorphic processes are the fundamental determinants of habitats a geomorphic/habitat approach provides a useful framework for vegetation studies. Linking habitat to geomorphic setting can also provide information on longevity, stability and dynamics of habitats, which can then be related to interpretations about the stage of development that a vegetation complex may have achieved.

Vegetation of wetlands in Australia, and in the Darling System of SW Australia specifically, has been classified according to the schemes described above. For instance, Riggert (1966) classified vegetated wetlands of the Darling System using terms such as meadow, marsh and swamp of Martin *et al* (1953). McComb & McComb (1967) applied fen and swamp, the terms of Tansley (1939), to wetland vegetation of Loch McNess, Yanchep. Pen (1983) applied the habitat-related term "riparian" to the river-flanking vegetation of the Swan-Canning system. Cresswell & Bridgewater (1985) used the approach of Braun-Blanquet (1932) to divide wetland vegetation into community types.

All the overseas and local classifications are not totally satisfactory for categorising wetland vegetation of the Darling System, considering the complex nature of wetlands. Each scheme has some positive attributes, such as categorization either of structure or of floristics, but no one system conveys information about size, extent and organization of a wetland vegetation complex, features that we consider important in descriptive studies, ecological studies, comparative work for use in conservation, or assessment of fauna habitats (Golet & Larsen 1976). To this objective, a new approach to the categorization of wetland vegetation for the Darling System is presented below.

The proposed classification

The objectives of a classification designed specifically for wetland vegetation are:

- to present a simplified picture of the structure and organization of wetland vegetation. Use of physiognomic categories are relevant here because they suggest an immediate picture of structural forms (particularly density and height of plant cover, and dominant life forms);
- to relate suites of vegetation communities or physiognomic types either to a given type of wetland or to habitats and edaphic features, such as geomorphology and hydrology within wetlands;
- to use data on wetlands in order to compare the type and extent of patterns between different wetland areas;
- to place wetlands at a stage in their development; and
- to convey information on the size and extent of the wetland vegetation complex.

The practical guidelines of any classification system also are clarified below before setting out the proposed scheme. In this instance, for wetland vegetation, the most pertinent guidelines are: direct observation should be the basis of data collection and analysis; classes should be few and should incorporate a simple nomenclature system (hence floristic terms at species level should be avoided to facilitate effective communication by widespread usage); classes should be such that cartographic representation is manageable; and the framework should be flexible enough to encompass any major changes or alteration to wetlands.

The approach adopted in this paper entails systematically determining the following attributes: 1) scale of the wetland vegetation complex; 2) areal extent and pattern of distribution of vegetation cover over the wetland; 3) internal organization of the vegetation in plan; 4) predominant vegetation structure, or the range of structural types in zones; and 5) details of the structure and floristics of vegetation, used in combination as an adjunct.

Combinations of attributes 2 & 3 result in the identification of nine primary categories of wetland vegetation systems as defined in this paper. These categories are used with the structural classification of Specht (1970, 1981) to provide a binary system of nomenclature, which forms the core of the classification. Scale terms are added as adjectival qualifiers, and details of floristics and structure in combination may be added as an inventory in a secondary classification to the main binary classification, if required (Fig. 1).

Scale terms

Because wetlands and their vegetation cover usually are discrete entities (surrounded and bounded by uplands), descriptive scale terms to denote size can be readily applied. Terms of scale to describe wetland vegetation are (adapted from Semeniuk 1987):

Mega — wetland complex larger than a frame of reference 10 km x 10 km.

Macro — wetland complex encompassed by a frame of reference 1000 m x 1000 m to 10 km x 10 km.

Meso — wetland complex encompassed by a frame of reference 500 m x 500 m to 1000 m x 1000 m.

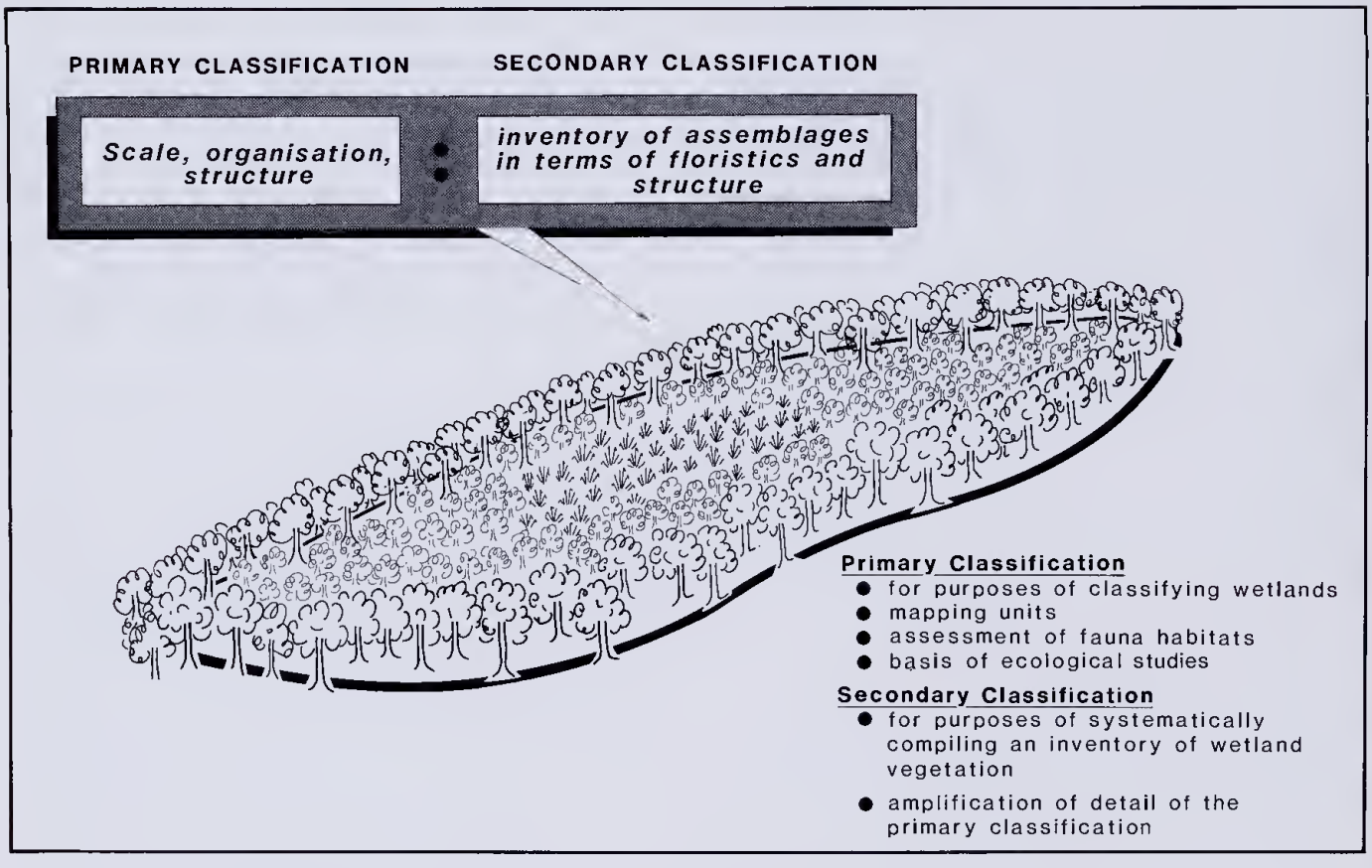


Figure 1 Conceptual diagram showing the elements of the proposed classification and its uses.

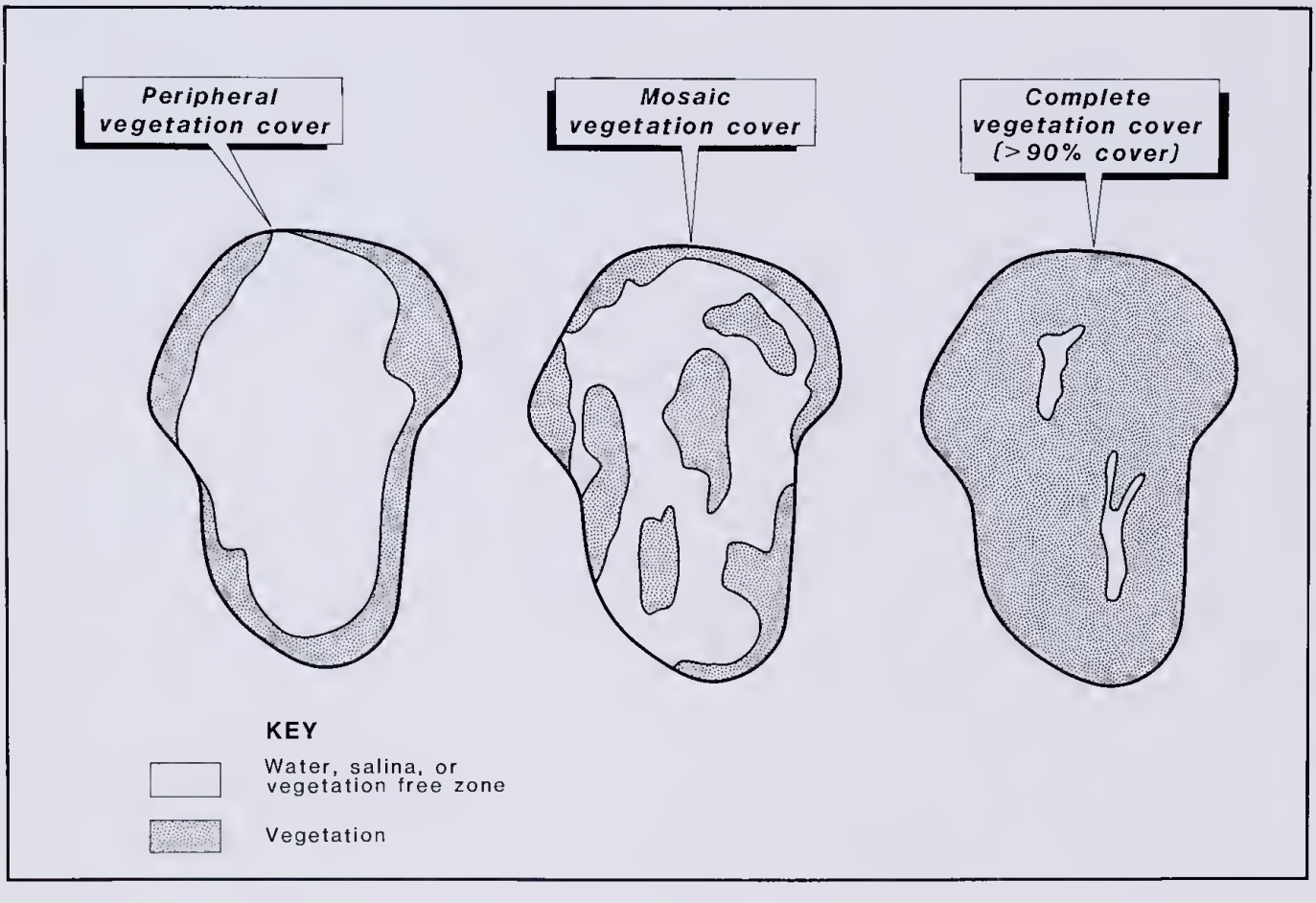


Figure 2 The three categories of vegetation cover.

Micro — wetland complex encompassed by a frame of reference 100 m x 100 m to 500 m x 500 m.

Lepto — wetland complex smaller than a frame of reference 100 m x 100 m.

Analysis of vegetation cover

The relative proportions of vegetation cover and open water (cf Golet & Larson 1976), and their spatial arrangement are considered in this section. Only emergent, perennial, woody or herbaceous macrophytes are considered in this vegetation classification. Submerged aquatic angiosperm and algal vegetation (submergents) are not directly included in the classification. However, their presence is implied wherever there is free standing water, and the extent of free water is incorporated and implied in the nomenclature of the vegetation cover. For instance, lakes with permanent water and sumplands with seasonal water support various permanent or seasonal submergents. The difficulties in dealing with submergents are that they are not readily observable by field survey and aerial photographic mapping, or they may have highly seasonal population dynamics, or they may be partly free-floating and hence not readily relatable to a vegetation zone.

Wetland vegetation cover is described in two ways, firstly by extent of cover, and secondly by the complexity of organization (*cf* Golet & Larson 1976). The category 'unvegetated' is not used in this classification. The vegetation cover is classified as (Figs 2 & 3): peripheral, mosaic, and complete. The classes are gradational into each other, but there is no implication that the classes necessarily reflect increasing percentage cover. For instance, vegetation covering 50% of a wetland in a pattern of mosaics needs to be differentiated from vegetation that concentrically fringes a wetland leaving 50% of open water. Thus the use of percentage cover has been deliberately avoided when erecting classes. This ensures that the proposed categories convey information on the pattern of vegetation type, which has implications for wetland seral development. However, a boundary of 90% cover is used to define the limit between the categories of total cover and patchy to peripheral cover (Fig. 3).

Assemblages, or communities, in wetlands are recognized on the basis of structure and floristics. The pattern of the vegetation types within the wetlands is classified as: homogeneous, zoned, or heterogeneous (*ie* in patches). Wetlands with a single vegetation assemblage comprise homogeneous vegetation types. Wetlands with a combination of assemblages can be further differentiated into either zoned or heterogeneous types, depending on the organization of the assemblages within the wetland complex. The combination of areal extent and internal organization of the wetland vegetation results in the recognition of 9 basic wetland categories:

	Areal extent of vegetation cover		
Organization of vegetation	**Peripheral**	**Mosaic**	**Complete** (>90%)
Homogeneous	Periform	Paniform	Latiform
Zoned	Zoniform	Gradiform	Concentriform
Heterogeneous	Bacataform	Heteroform	Maculiform

These terms form the primary part of the binary terminology proposed in this paper. The definitions, etymology and rationale for the terms are presented in Table 1.

Table 1

Definitions and etymology of terms for types of vegetation cover

Term	Definition	Etymology
Latiform	vegetation which entirely covers the wetland and is homogeneous in structure & composition.	from Latin, *latus*, broad or extensive; here describes extensive vegetation cover
Paniform	vegetation which occurs in patches, or in mosaics, or as islands, but which is homogeneous.	from Latin, *pannus*, a patch; here describes the patchy or mottled nature of vegetation cover
Periform	vegetation which is peripheral & homogeneous.	from Greek, peris, around or girdling; here describes the peripheral nature of vegetation cover
Concentriform	vegetation which entirely covers the wetland & is concentrically zoned in structure and/or composition; zonation may be symmetric or asymmetric.	from Latin, *concentricus*, concentric; here describes complete cover wherein there is clear concentric zonal pattern
Gradiform	vegetation which occurs in patches, or in mosaics, or as islands, but which is overall zoned.	from Latin, *gradus*, a gradation; in here describes mosaic vegetation exhibiting gradual zonation
Zoniform	vegetation which is peripheral & concentrically zoned; zonation may be symmetric or asymmetric.	from Latin, *zonae*, terrestrial zones; in here describes peripheral vegetation showing zonal pattern.
Maculiform	vegetation that completely covers a wetland, but composed of mosaics of associations.	from Latin, *maculosus*, speckled; here describes complete vegetation cover that is in mosaics
Heteroform	mosaic cover composed of a patchwork of associations.	from Greek, heteros, different or mixed; here describes vegetation that is patchy in cover, and composed of a patchwork or mosaic of assemblages
Bacataform	peripheral cover composed of a patchwork of associations	from Latin, *bacatus*, set with beads; in here describes peripheral vegetation that is in mosaics, resembling a ring of beads

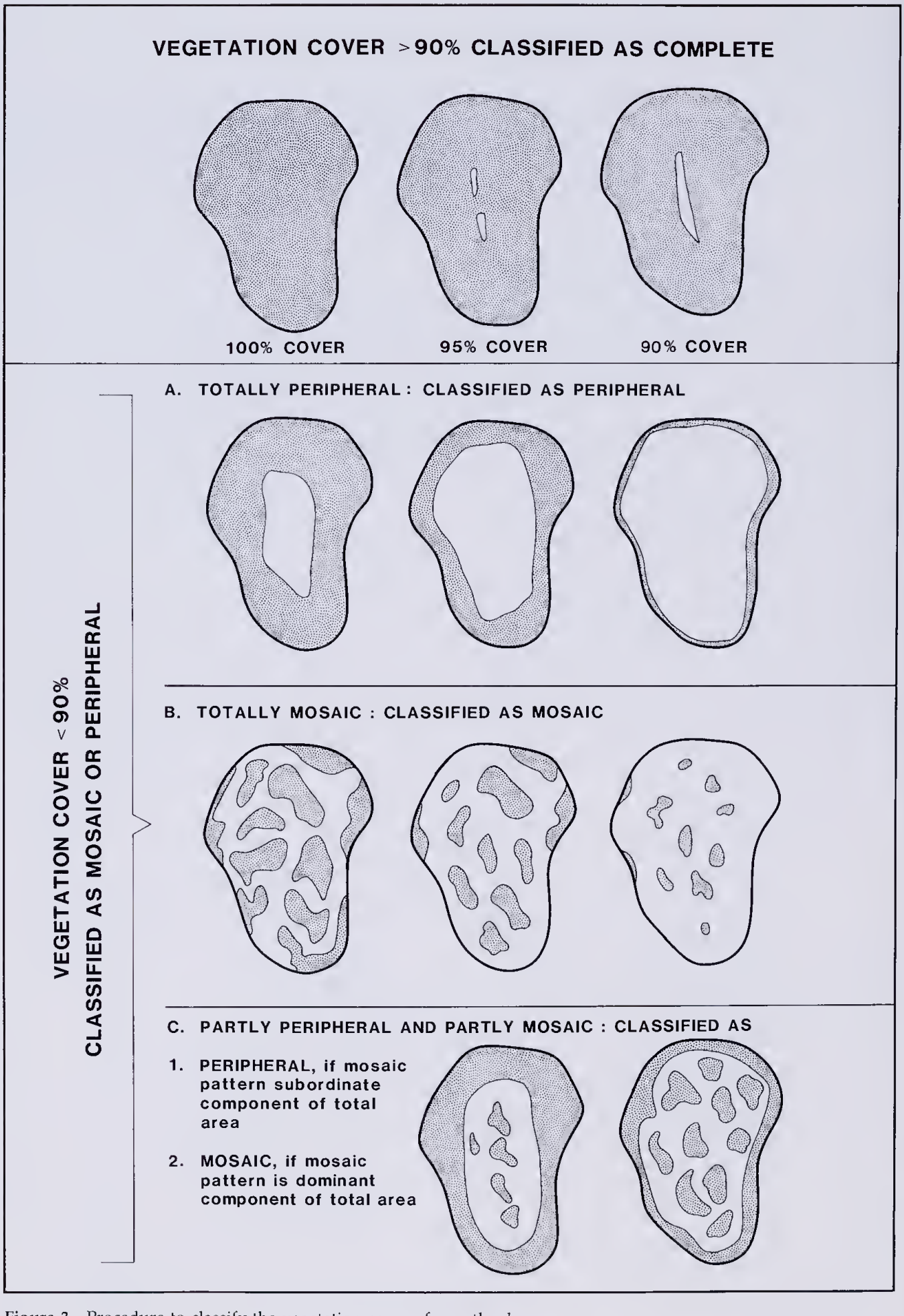


Figure 3 Procedure to classify the vegetation cover of a wetland.

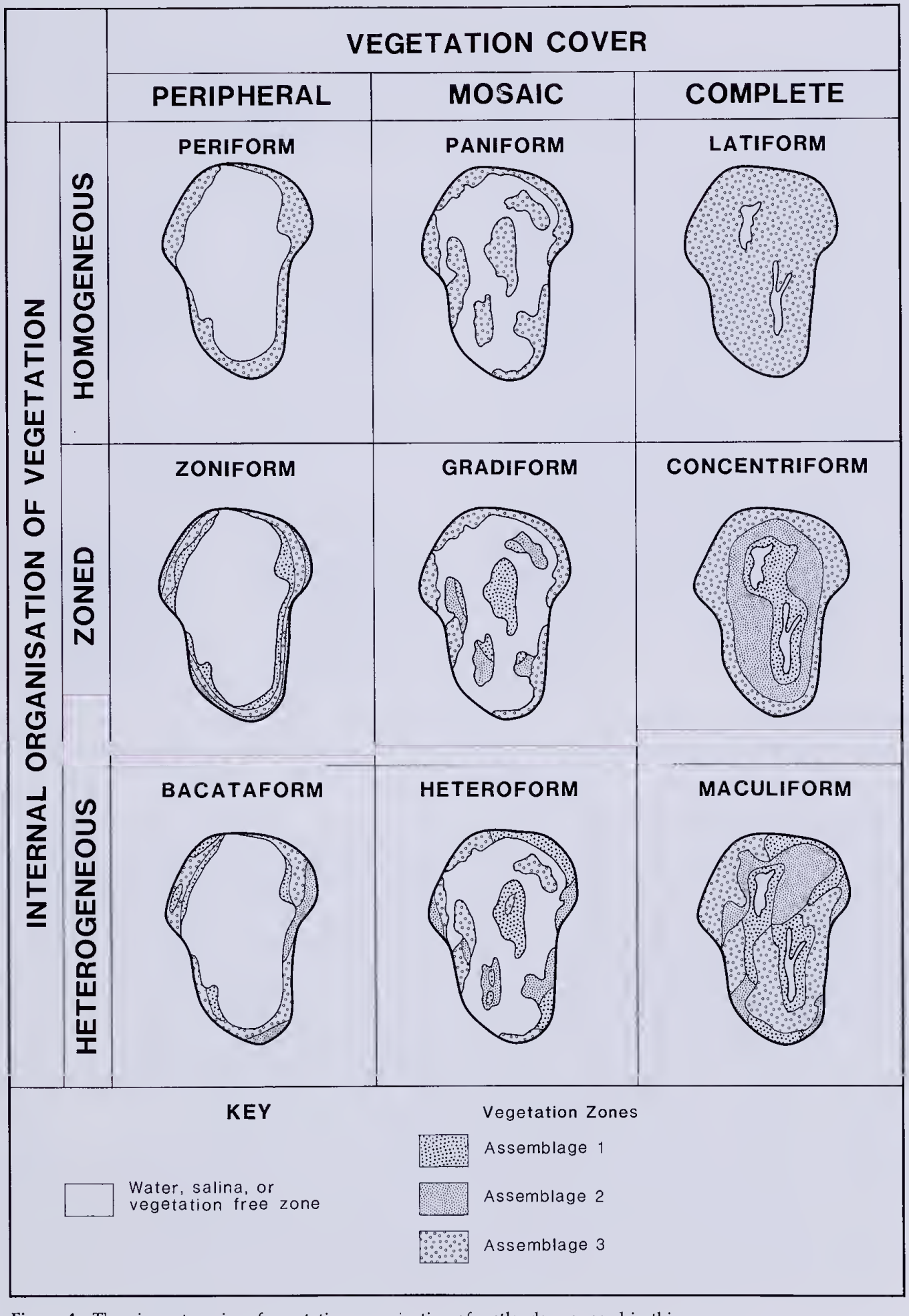


Figure 4 The nine categories of vegetation organization of wetlands proposed in this paper.

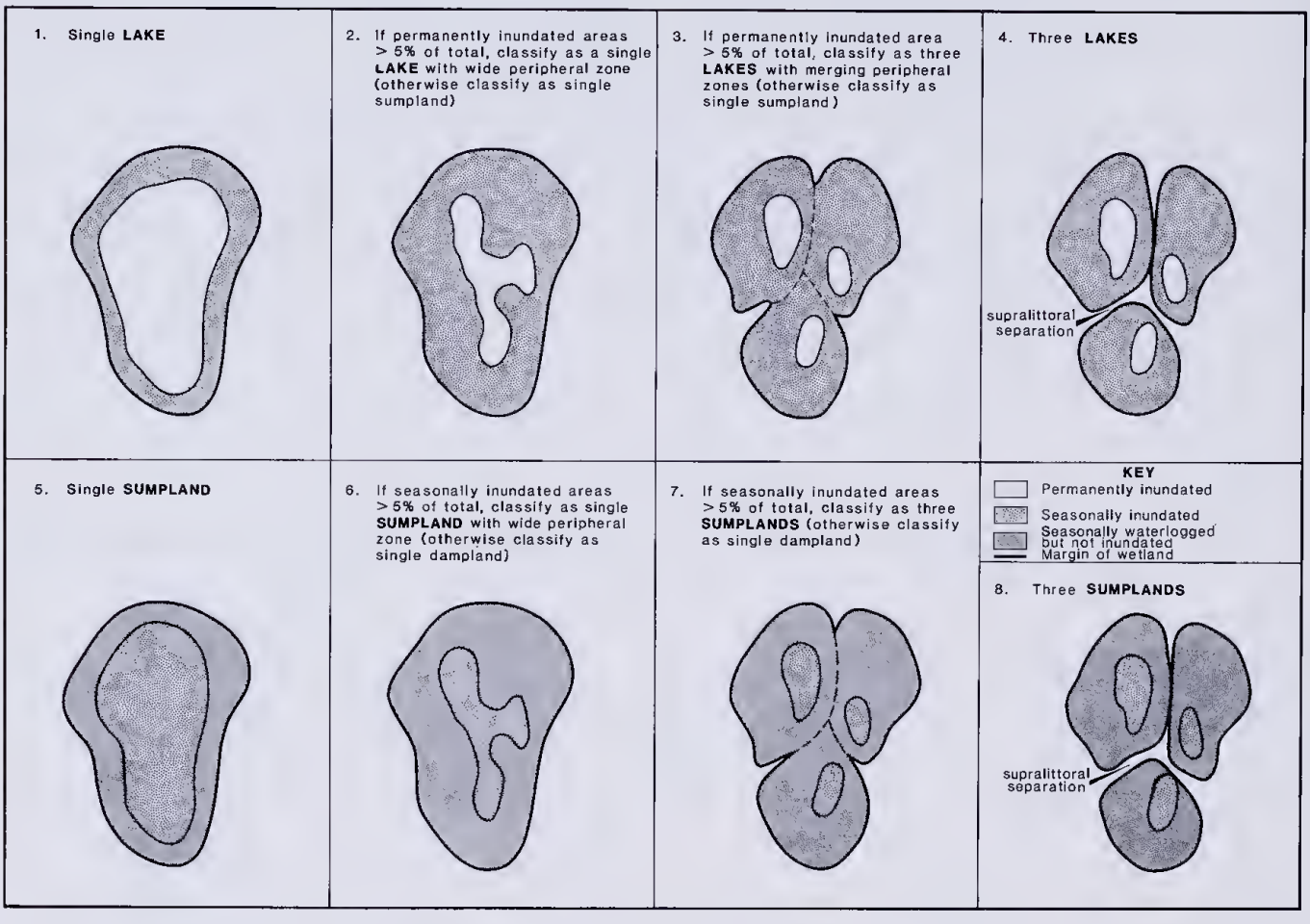


Figure 5 Diagram illustrating the procedure to separate single wetlands from merging wetlands and from closely occurring clusters of wetlands.

In recognizing mottled vegetation patterns it becomes necessary to distinguish between wetlands that internally either have multiple wetter zones, or have patches of distinct assemblages within a relatively homogeneous edaphic setting, from those that are separate individual basins but which are laterally coalescing or nearly merging (Fig. 5). For purposes of this paper a large clearly defined wetland with a number of separate wetter basin centres is separated from a system of smaller wetlands whose margins and supralittoral vegetation zones overlap. Clearly the vegetation of the former would be classified as maculiform, whereas the vegetation in the latter would be classified according to the organization of the separate individual wetlands. We recognize 2 important factors to aid in separating the two types of wetland systems described above (Fig. 5). One factor is the occurrence of 'damp' land, supralittoral, or upland units as flats or ridges separating the wetter basin centres within a wetland complex, and the other is the ratio of area of basin centre to total wetland area. If the wetter centres within a wetland complex are separated by seasonally water-covered littoral zones then the entire wetland is treated as one unit. If the areas separating the wetter basin centres are comprised of dryland, or damp soil vegetation zones, then the wetland complex should be treated as being comprised of numerous separate wetland entities.

Structure

The structural terms of Specht (1981) are adopted here to refer to the structure of wetland communities. These terms form the second part of the binary terminology. The structural dominants within a community are the focus of assessment, although it is recognized by Specht (1981) and Beard & Webb (1974) that further subdivision may be based on species that are numerically dominant or visually dominant. In the instance where the community exhibits more than one structural type with none predominating, the terms "mixed" structure, or "layered" structure is used. Specht (1981) defines the latter term to denote "two or more strata prominent'. In this paper the term "layered" is used in conjunction with one of the established structural terms, with the uppermost stratum providing the key term. For example, a forest with understory of shrubs and grasses is termed "layered forest'.

Where the wetland vegetation system is composed of several structural types arranged in zonal pattern, these are listed in order of their occurrence from margin to centre of the wetland, essentially mirroring some environmental gradient (Fig. 6). The listing of structural types within a heterogeneous system, where there is patchy distribution of mosaics of differing vegetation, also should be in order of occurrence from margin to centre. Thus a wetland complex composed of peripheral forests with no internal

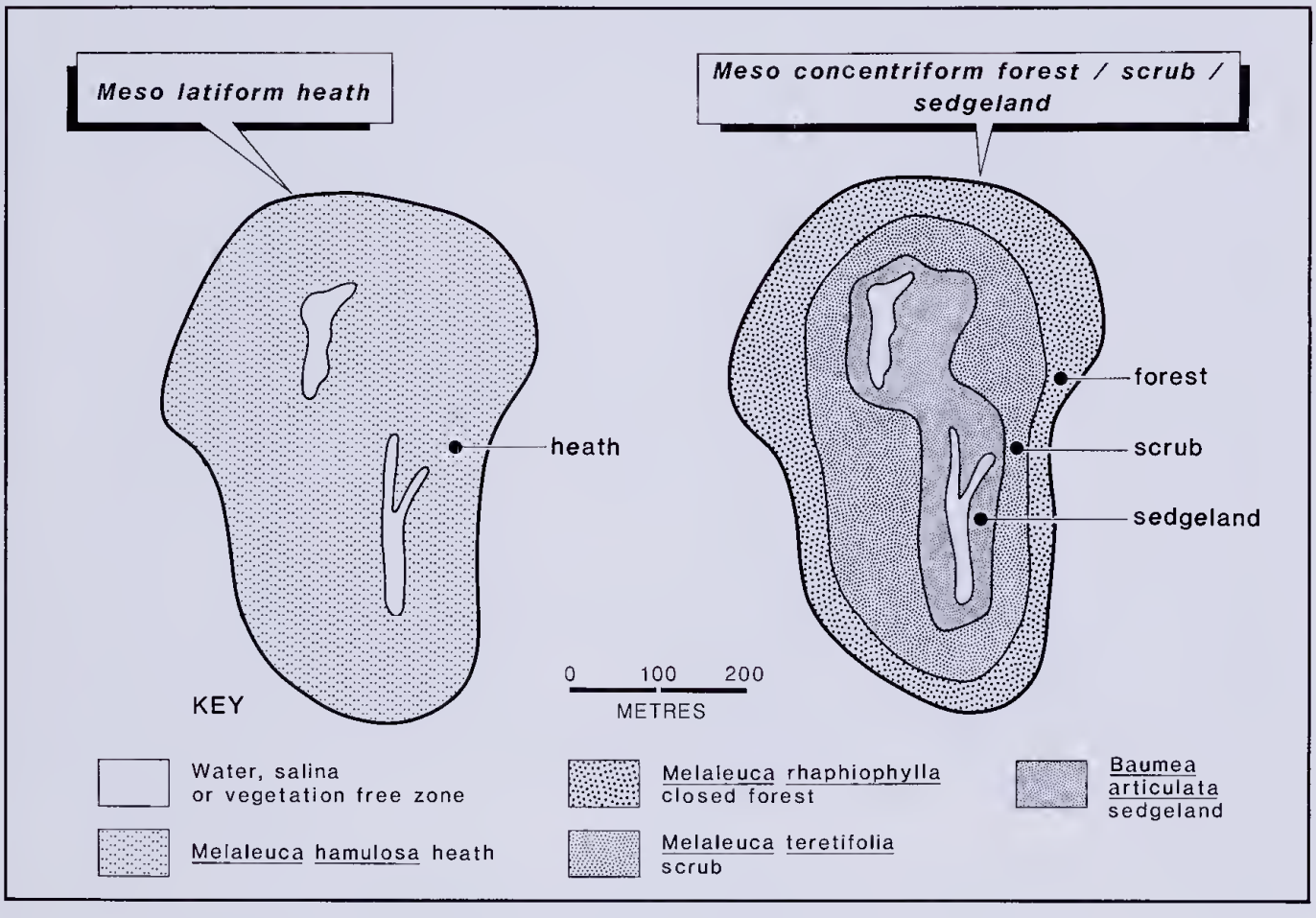


Figure 6 Conceptual diagram showing the classification of two types of internal vegetation organization on wetlands of essentially similar size, shape and amount of vegetation cover.

organization of communities would be termed *periform forest*. A system of zoned peripheral vegetation composed of forests grading to heaths and sedges in the wetland centre would be a *zoniform forest/heath/sedgeland*. A system of vegetation that forms patchy cover over the wetland, with little differentiation of zones but with a mosaic of differing vegetation types that include sedgeland, scrub and heath (in that order of abundance) would be termed *heteroform sedgeland/scrub/heath*.

Floristics (and structure) of assemblages

Once the overall scale, organization and structure of wetland vegetation have been classified, detailed characterization of the various component assemblages in terms of their floristics (and structure) can be undertaken. Cresswell & Bridgewater (1985) described a range of vegetation communities in wetlands for the Perth Metropolitan Region, and these can form the basis for the floristic categories. Structural terms need only be applied for the community terms of Cresswell & Bridgewater (1985) for them to be adequate for use in this paper. However, because the study of Cresswell & Bridgewater (1985) did not extend outside of the Perth Metropolitan Region, their categories do not cover all wetland assemblages or communities in the Darling System. Accordingly, a provisional listing of the main wetland assemblages in the study area, together with a brief description of their floristics and structure drawn from Cresswell & Bridgewater (1985) and supplemented by our study, is presented in Table 2. This information thus extends the results of Cresswell & Bridgewater (1985).

Alternatively, it also is possible to add information on the sequence of assemblages in a wetland by listing the (floristics and structure of) assemblages in an inventory form using the triplet notation approach of Beard & Webb (1974) and Beard (1981). With this approach, for instance, a sequence of assemblages consisting of *Melaleuca preissiana* closed low forest, followed down-slope by *Astartea fascicularis* closed thicket, and then *Baumea articulata* sedgeland, would be notated as mLd/a_sSd/bGc, where m = *Melaleuca preissiana*, a_s = *Astartea fascicularis* and b = *Baumea articulata*, L = low tree, S = shrub and G = sedgeland, and d = dense canopy and c = mid-dense canopy. Because of the range of floristic assemblages present in wetlands in the Darling System, an additional range of notations would have to be devised to extend those relating to wetland formations as covered at present in Table VII of Beard (1981). It is beyond the scope of this paper, however, to devise a scheme covering the full range of wetland vegetation assemblages.

The information on the floristics of the assemblages may be added to the main binary wetland classification terminology as a suffix, or secondary adjunct, to convey

Table 2

The most common wetland assemblages and their floristic/structural components

Assemblage[1]	Main structure	Floristics[2]	Correlation with communities of Cresswell & Bridgewater 1985
Acacia spp	closed scrub	*Acacia* spp	no equivalent community
Astartea fascicularis	closed heath	*A. fascicularis*, *Aotus gracillima*	no equivalent community
Baumea articulata	closed sedgeland	*B. articulata*	*Baumea articulata* community
Baumea juncea	closed sedgeland	*B. juncea*, *Gahnia trifida*	*Centella asiatica* community
Eucalyptus rudis	closed low forest low woodland	*E. rudis*	no equivalent community
Homalospermum firmum	closed heath	*H. firmum*	no equivalent community
Juncus kraussii	closed sedgeland	*J. kraussii*	*J. kraussii* community
Kunzea ericifolia	closed scrub	*K. ericifolia*	no equivalent community
Lepidosperma gladiatum	closed sedgeland	*L. gladiatum*	no equivalent community
Melaleuca rhaphiophylla	closed low forest open low forest closed scrub	*M. rhaphiophylla*, with variable understories of *B. articulata*, *B. juncea*, *J. kraussii*, *M. teretifolia M. hamulosa*, *M. lateritia*, *Typha orientalis*	mostly equivalent to *Melaleuca rhaphiophylla* community, and parts of the *Juncus kraussii* complex
M. rhaphiophylla-Eucalyptus rudis	closed forest	*M. rhaphiophylla*, *E. rudis*	*Melaleuca rhaphiophylla - Eucalyptus rudis* complex
M. rhaphiophylla-M. cuticularis	closed low forest open low forest	*M. rhaphiophylla*, *M. cuticularis*, with variable understories of *Halosarcia halocnemoides*, *Suaeda australis*, *J. kraussii*, *M. hamulosa*, *M. leptoclada*, *M. incana*, *Gahnia trifida*	no equivalent community
M. cuticularis	closed scrub	*M. cuticularis*, with variable understories of *H. halocnemoides*, *Suaeda australis*, *Sarcocornia quinqueflora*, *J. kraussi*	*Melaleuca cuticularis* complex
M. preissiana	closed low forest closed scrub woodland open woodland	*M. preissiana*, with variable understories of *Astartea fascicularis*, *Agonis linearifolia*, *H. firmum*, *Hypocalymma angustifolia*, *Xanthorrhoea preissi*, *Regelia inops*, *Viminaria juncea*	no equivalent community
M. preissiana - Banksia littoralis	closed low forest closed scrub woodland open woodland	*M. preissiana* & *B. littoralis* with variable understories of *Astartea fascicularis*, *Agonis linearifolia*, *H. firmum*, *Hypocalymma angustifolia*, *Xanthorrhoea preissi*, *Regelia inops*, *Viminaria juncea*	part of the *Banksia littoralis - Melaleuca preissiana* sub-community
M. teretifolia	closed scrub closed heath	*M. teretifolia*	*Melaleuca teretifolia* community
M. teretifolia-M. lateritia	closed heath	*M. teretifolia*, *M. lateritia*, *Calothamnus lateralis*, *Hakea varia*	no equivalent community
M. hamulosa	closed scrub shrubland	*M. hamulosa*	no equivalent community
M. uncinata	closed scrub	*M. uncinata*	no equivalent community
Mixed *Melaleuca*	closed heath	*M. teretifolia*, *M. lateritia* *M. incana*, *M. leptoclada*	no equivalent community
Regelia inops	closed scrub	*R. inops*	no equivalent community
Typha orientalis	closed sedgeland	T. orientalis	*Typha orientalis* community

[1] These units are not intended to include the gradations between assemblages where two vegetation assemblages adjoin.
[2] This list is of visual or structural dominants, and is not intended as an exhaustive inventory.

inventory information. In essence this approach provides a structured way in which to systematically describe and compile an inventory of wetland vegetation units. The order of listing of the floristic and structural terms for each assemblage, if the wetland vegetation complex is composed of more than one assemblage, is in an order following the structural sequence (Fig. 6).

Application of the classification

The classification is applied in sequence as follows:

1) determine the scale of the wetland complex,
2) determine the extent of the vegetation cover as either peripheral, mosaic or complete,
3) determine the internal organization of the vegetation as either homogeneous, zoned or heterogeneous,
4) determine the structure of the vegetation zones, and
5) determine the floristics of the vegetation zones.

We emphasize that the extent and type of distribution of vegetation cover must be determined *before* the type of internal organization of the cover is determined.

Vegetation maps from several areas in different physiographic settings within the Darling System are presented in Figure 7 to illustrate the practical use of the proposed classification, and to present examples of the variety of wetlands with differing types of vegetation. A typical range of basin wetland vegetation within the Darling System is fully classified in Table 3.

Discussion

The advantages of classifying wetland vegetation as proposed in this paper are manifold. First, the classification creates a conceptual picture of the wetland vegetation, and the diversity and complexity of vegetation of specific wetlands then become obvious. It also allows for wetlands to be classified and thus easily mapped. The classification further can highlight wetland vegetation systems that are simple, or complex and diverse, with implications for wildlife habitats and management in that the results can be used in studies of wetlands for comparative purposes. The various categories of wetland vegetation patterns brought out by the classification also can highlight underlying ecological and edaphic patterns.

To emphasize the habitat setting of any wetland vegetation complex, we suggest that the geomorphic term describing the wetland (Semeniuk 1987) be incorporated into the nomenclature (*eg* mega periform *sumpland* forest, or meso latiform *dampland* heath). Use of the geomorphic term in the classification would indicate the types of vegetation that could be expected in the wetland. This is because the various vegetation assemblages are closely linked to type of wetland (*eg* lake *vs* sumpland *vs* dampland), and its internal gradients (*eg* whether it is edaphically zoned, heterogeneous, or homogeneous).

Table 3

Classification of the vegetation of some typical wetlands

Wetland	Type	Classification of vegetation	Inventory of assemblages[1]
Lake Mungala	sumpland	micro zoniform woodland/low forest/shrubland	*M.preissiana/M.rhaphiophylla/M. teretifolia*
Bindiar Lake	dampland	meso concentriform forest/sedgeland	*M. preissiana-B.littoralis/E. rudis/?Leptocarpus*
Lake Pinjar	sumpland	mega maculiform closed low forest/heath/ sedgeland	*M. rhaphiophylla/E. rudis/M. preissiana/M. teretifolia/ Lepidosperma* sp/*B. articulata*
Lake Joondalup	lake	macro zoniform closed low forest/sedgeland	*M. rhaphiophylla-E. rudis/B. articulata-T. orientalis*
Lake Jandabup	lake	macro bacataform open woodland/sedgeland	*M. preissiana/ B. articulata/Baumea-Juncus-Lepidosperma-Leptocarpus-Typha*
Lake Gnangara	sumpland	macro zoniform open woodland/open forest	*M. preissiana/M. rhaphiophylla Baumea-Juncus-Lepidosperma-Leptocarpus-Typha*
Lake Carabooda	sumpland	macro maculiform open low forest/tall scrub/ sedgeland	*M. rhaphiophylla/E. rudis-B. littoralis/T. orientalis*
Lake Booroogoon	sumpland	micro periform closed low forest	*M. rhaphiophylla*
Roe Swamp	sumpland	micro maculiform woodland-closed forest/scrub/ sedgeland	*M. preissiana/M. preissiana-E. rudis/K. ericifolia/M. rhaphiophylla/M. teretifolia/T. orientalis*
Lake Coogee	sumpland	meso zoniform closed low forest/scrub/herbland	*M. rhaphiophylla/M.cuticularis-H. halocnemoides*
Lake Thompson	lake	macro zoniform closed low forest/closed scrub/ grassland/sedgeland	*M. preissiana/M. preissiana-E. rudis/E. rudis/Acacia saligna/B. articulata-T. orientalis*
Forrestdale Lake	sumpland	macro zoniform low forest/sedgeland	*M. rhaphiophylla-E. rudis/T. orientalis-J. kraussii*
Brownman Swamps	sumplands	macro latiform open low forest	*M. rhaphiophylla*
The Spectacles	sumplands	macro maculiform open woodland/closed scrub/ closed heath/closed low forest	*M. preissiana/E. rudis/*mixed *Melaleuca/M. rhaphiophylla*
Stable Swamp	sumpland	macro bacataform closed low forest/closed scrub/ sedgeland	*M. rhaphiophylla/M.teretifolia/B. articulata/B. juncea*
Pt Becher wetlands	sumplands	lepto concentriform sedgeland	*L. gladiatum/L. angustifolium/I. nodosus*

[1] The various assemblages are separated by a slash (/).
[2] Some of the species of sedge identified in the inventory of assemblages are provisional, because of the difficulty of identifying sedge taxa.

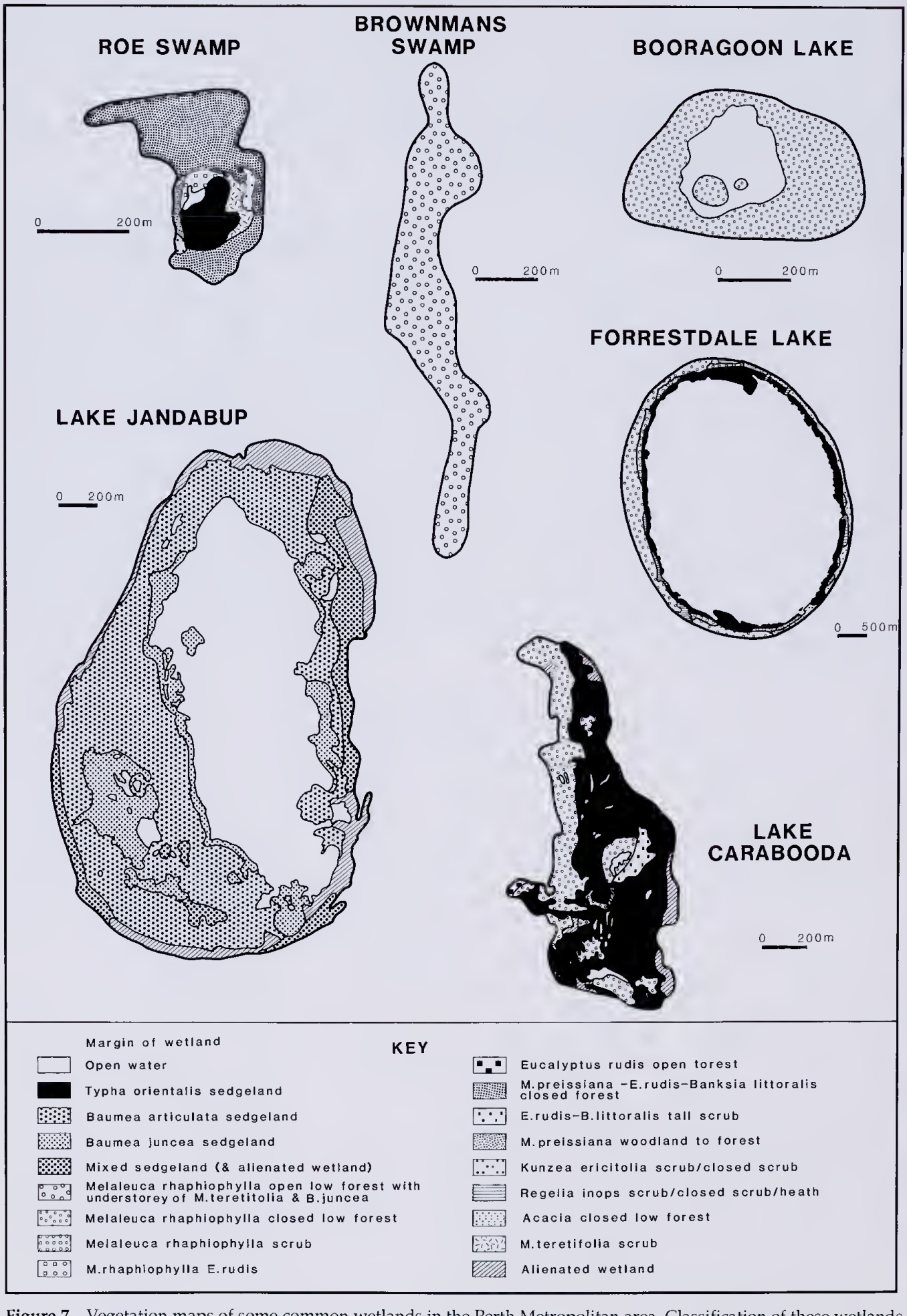


Figure 7 Vegetation maps of some common wetlands in the Perth Metropolitan area. Classification of these wetlands is presented in Table 3.

Finally, the classification categories presented in this paper may be used, if required, as qualifiers to existing wetland classifications. For instance, Semeniuk (1987) suggested that a terminology describing vegetation patterns could be used as a tertiary or quaternary qualifier to the wetland types identified primarily on physical attributes. If only the overall vegetation pattern of a wetland needs to be noted as a descriptive qualifier, there may be no need to list the sequence of structural types, and the vegetation classification presented in this paper may be modified to adjectival form, with the substitution of "form" in the nomenclature by "phytic'. Thus a lake with periform forest, a sumpland with gradiform heath/sedgeland, and a dampland with zoniform forest/heath/sedgeland could be termed periphytic lake, gradiphytic sumpland and zoniphytic dampland, respectively. In these cases the emphasis is on the classification of the wetland type, and the vegetation adjectival qualifier simply augments the nomenclature of the wetland.

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VOLUME 72 (PART 4)

CONTENTS VOLUME 72 PART 4 1990

	Page
Natural products from Western Australian marine organisms **E L Ghisalberti & P R Jefferies**	95
Wetlands of the Darling System, Southwestern Australia: a descriptive classification using vegetation pattern and form **C A Semeniuk, V Semeniuk, I D Cresswell & N G Marchant**	109

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